THE CRANIAL FORAMINA OF PROTROGOMORPHOUS RODENTS; AN ANATOMICAL AND PHYLOGENETIC STUDY

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Dedicated to
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LIST OF FIGURES

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ABSTRACT. The cranial foramina and the blood vessels and nerves passing through them are described in detail for the sciurid genus *Marmota;* this data serves as the basis for understanding structures seen in the fossils. The cranial foramina are described and compared in North American specimens of the protrogomorphous rodent families Paramyidae, Sciuravidae, Ischyromyidae, Cylindrodontidae, Prosciuridae, Aplodontidae, and Mylagaulidae. The least variable foramina are those that transmit nerves; the most variable, veins. Presence or absence, relative position, number, and relative size of foramina are useful characters in determining relationships. Within the Paramyidae differences indicate an early radiation of lineages. Paramyids and sciuravids have many primitive features in common, but differ in several details; of especial interest in these families are the pathways of the internal carotid artery and its branches. Peculiarities common to the foramina of ischyromyids and cylindrodontids suggest that the two groups can be made subfamilies of the family Ischyromyidae. The Prosciuridae are included likewise with the Aplodontidae and Mylagaulidae in the Aplodontoidea.

INTRODUCTION

The origin of the Rodentia and their successful radiation can be attributed to a unique design for gnawing and chewing. Perfection of the design has involved modification of the jaw and skull for more efficient muscle configuration, and specialization of the incisors and cheek teeth in response to the multitude of specific niches into which rodents have diversified. The masticatory system has been subjected to great selection pressure and has been modified from the original design in ways that were limited by genetic potential and by the efficiency of certain modifications relative to others. These are the principal reasons for the parallelism so typical of rodent phylogeny.

To date, the classification of rodents has been based primarily on the structure of the masticatory muscles, the infraorbital foramen, the lower jaw, and the cheek teeth. These characters are all part of the masticatory system, and, when traced through time, their observed modifications reveal a complex phylogeny. Gaps in the sequence, however, cannot always be filled. Whole families of rodents stand in uncertain relationships to proposed phylogenies. This situation is not surprising; in a phase of rapid evolution a gap of a few million years is enough to permit a discrete group to appear full-blown in the fossil record. The ancestry of such a group is often unclear because of parallelism among the earlier lineages from which it could have descended.

The cranial foramina, unlike the components of the masticatory apparatus, are not part of a single functional system. There is no reason to suppose that selection acts on them as a unit or that selection pressure from the external environment acts on them directly. In the main, foramina serve a passive function; they permit nerves and blood vessels to pass through the bones of the skull. It is reasonable to suppose that foramina may vary in position and soft-part content so long as they satisfy the requirements of the circulatory and nervous systems. Within these limits selection is unimportant, and changes fixed in a small population by random genetic processes will characterize a new lineage arising from it. Fusion and division of foramina are possible examples.

The position or the existence of foramina may be changed as they are impinged upon by other structures. Foramina in the orbit are modified to lead around the roots of high-crowned cheek teeth. In the temporal region they may be closed off by enlarged bullae, and some other combination of foramina then acquires their function.

A foramen may be taken over by a different functional system. The infraorbital foramen has been seized upon in the hystricomorphous and myomorphous rodents for transmission of a part of the medial masseter muscle. From the moment of seizure it ceased to behave solely as the foramen it was and came under the influence of the selective forces acting upon the masticatory system. The tough connective tissue around a foramen may change to accommodate a new structure. In those sciurids which lack an infraorbital canal, a tough membrane shielding the transmitted nerves and vessels from the lateral division of the masseter takes its place.

Hill (1935 and 1937), Guthrie (1963 and 1969), and Bugge (1970, 1971a, b, and c) have been the principal contributors to knowledge of cranial foramina and the cephalic nervous and vascular systems in living rodents. They describe differences that appear to have a systematic basis. But the very nature of their work, limited primarily to modern examples, precludes discernment of the primitive and derived conditions for each aperture. The pattern of evolution can be seen with certainty only when the time-dimension of paleontology is added. Detailed consideration of the fossils indicates which features in a group are primitive and eliminates the need to

rely on a so-called, but not in fact, primitive living genus such as *Aplodontia*.

This paper on the protrogomorphous North American rodents is the first half of my Ph.D. dissertation (Wahlert, 1972), which included the sciuromorphs also. Description of the cranial foramina in the latter families will be presented elsewhere, and I hope to extend the work to myomorphous and hystricomorphous forms. The Protrogomorpha as defined by Wood (1937 and 1955) contain the families Paramyidae and Sciuravidae, which are parts of the initial rodent radiation, and the derived families Cylindrodontidae, Ischyromyidae, Prosciuridae[1], Mylagaulidae, Aplodontidae, and Protoptychidae. *Protoptychus* was found to be both hystricomorphous and hystricognathus; a separate paper deals with its cranial and dental morphology (Wahlert, 1973).

This approach to the study of rodent evolution brings with it a special set of problems. The number of fossil skulls adequately preserved is very small in comparison with the number of forms known from teeth. The forms whose skulls can be examined include representatives of every family, but they may be from specialized side branches and not from the main lines of evolution. Most specimens are incomplete. The task of assembling data may be compared with that of a man in the dark who attempts to describe an exquisite topiary arabesque with only the aid of an unreliable flashlight.

The text is divided into sections, each dealing with a single taxon; for extinct lineages this is the family, and for surviving lineages, the superfamily. Sections are subdivided according to the importance of the included material and the completeness of the specimens.

Paramyid genera are considered sepa-

rately because many rodent lineages may have originated from within the family. Differences between genera may be critical in determining relationships to later forms, and it is important to recognize that information about cranial foramina in the fossils is quite uneven.

The genera within several families and even within a superfamily are enough alike that a single section describing each group is sufficient. The ischyromyids, cylindrodontids, prosciurids, and aplodontoids are treated in this manner.

Discussions at the end of each section compare features within the groups described and compare the most interesting features of the entire assemblage with those considered in preceding sections.

The bearing of the evidence provided by cranial foramina on the phylogeny and relationships of North American protrogomorphous rodents is discussed in the conclusion.

A list of the specimens examined is presented at the beginning of each section or subsection. Definitions of the stratigraphic names can be found in Wood (H. E. Wood *et al.*, 1941) and Keroher (Keroher *et al.*, 1966; Keroher, 1970).

Abbreviations are as follows:

AMNH	American Museum of Natural History
CM	Carnegie Museum of Natural History
F:AM	Frick Collections, American Museum of Natural History
FMNH	Field Museum of Natural History
KU	University of Kansas Museum of Natural History
LACM (CIT)	Los Angeles County Museum (California Institute of Technology Collection)
MCZ	Museum of Comparative Zoology, Harvard University
USNM	National Museum of Natural History

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[1] I have followed Wilson (1949c) and assigned the prosciurids to a taxon of rank equal to the paramyid group. Wood places them in the Paramyidae as a subfamily.

SDSM   South Dakota School of Mines and Technology

UCMP   University of California Museum of Paleontology

UNSM   University of Nebraska State Museum

UOMNH   University of Oregon Museum of Natural History

YPM   Peabody Museum of Natural History, Yale University

A letter code, which follows each number, indicates the completeness of the fossil specimens:

s – whole skull   o – orbit
n – snout   t – pterygoid region
p – palate   c – cranium

A code such as npo indicates that the snout, palate, and orbit of the particular specimen are preserved and provided information for this study; the pterygoid region and cranium are either gone or are damaged and the detail destroyed.

Measurements of length were taken with a dial caliper calibrated to 1/20 mm. The diastemal length is a straight line measurement from the back of the incisor alveolus to the anteriormost edge of the alveolus of the first cheek tooth. The sizes of foramina smaller than 1.0 mm were estimated with a Dunlap spark-plug gauge.

Most of the figures were drawn with the aid of proportional dividers; enlargements of detail and outlines of small specimens were traced with a camera lucida microscope. I have made no attempt to show crenulations in the sutures but have taken care to illustrate the relationship of sutures to foramina. I have omitted detail from the teeth because excellent figures of the dentitions of all species studied are available in the literature. Solid lines indicate structures and sutures that I have seen in at least one specimen of the genus illustrated. Dashed lines indicate details that are less certain but probable in view of similar features in closely related forms. Dotted lines represent guesses. To some degree all the figures are restorations. I have attempted to eliminate distortions and to reconstruct all broken elements; the figures are not copies of the specimens. The key to abbreviations in the illustrations is given in the caption of Figure 1.

CRANIAL FORAMINA OF RODENTS WITH SPECIAL REFERENCE TO *MARMOTA*

Hill (1935) was the first to attempt a complete listing of the foramina in rodent skulls. From dissections and prepared skulls he described the position and contents of each foramen and stated how they differ

among several genera, but he gave no account of the circulatory and nervous systems themselves. Unless these systems are understood it is not possible to interpret and name several of the foramina. Tandler (1899, 1901, and 1902), Guthrie (1963 and 1969), and Bugge (1970, 1971a, b, and c) have examined the cephalic arterial circulation of various rodents, but, apart from Guthrie, these authors pay little attention to the foramina involved.

As an introduction to what follows, I present an account of the foramina and the circulatory system and cranial nerves in *Marmota monax* (Fig. 1). I follow Hyman (1942) and Greene (1935) for terminology of the soft parts. *Marmota* has several advantages for this purpose. Although fully sciuromorphous, it retains most of the cranial foramina met with in the earliest rodents, and the bones of the skull do not fuse in the adult.

Systems

CRANIAL NERVES

The hypoglossal (XII) emerges from one or more hypoglossal foramina and runs anteromedially into the base of the tongue. The foramina are situated just anterior to the occipital condyle on the ventral side of the skull.

The vagus (X), accessory (XI), and glossopharyngeal (IX) emerge from the jugular foramen. It is between the bulla and the basioccipital and is lenticular in shape.

The facial (VII) emerges from the stylomastoid foramen deep between the mastoid process and the bulla. The main part of the nerve runs anteriorly and diversifies over the masseter muscle. The chorda tympani branch of the facial emerges from a tiny slot, the canal of Huguier, in the front surface of the bulla. It runs anteromedially to join the lingual branch of the trigeminal (V) nerve.

The mandibular division (3rd) of the trigeminal nerve (V) emerges from the large foramen ovale in the pterygoid region. Initially it runs anterolaterally through a notch in the lateral pterygoid flange. A strut of bone may cross the notch to form a foramen which I am calling the foramen ovale accessorius. The strut separates the mandibular nerve and its internal pterygoid branch. The auriculotemporal branch diverges just outside the foramen ovale. The mandibular nerve continues around the outside of the external pterygoid muscle and splits into three parts. The inferior alveolar branch enters the mandibular canal of the lower jaw. The mylohyoid and lingual, which is joined by the chorda tympani, run around the muscle and turn medially into the soft tissue.

Two portions of the mandibular division, the masseteric and buccinator nerves, run dorsolaterally from the foramen ovale through a canal in the alisphenoid bone; the canal shares its posterior opening with the alisphenoid canal, but runs through the bone above it. These nerves emerge on the side of the head. Both nerves may pass through one foramen or each through its own (masticatory and buccinator foramina); the two cases can occur together on opposite sides of a single skull. The buccinator nerve runs anteriorly, but a small branch turns back on leaving the foramen. The masseteric nerve also has two branches; the smaller runs dorsally to the temporal muscle. The main part remains against the alisphenoid region in a shallow vertical channel. When this branch reaches the front of the posterior root of the zygoma, it turns laterally, passes through mandibular notch of the jaw, and descends to the masseter muscle.

The maxillary division (2nd) of the trigeminal nerve enters the orbit through the sphenoidal fissure. On cutting away the lateral surface of the alisphenoid region, the alisphenoid canal is exposed. Two large branches of the maxillary enter the canal dorsally through two large foramina; the small zygomatic branch emerges in some cases from a separate small foramen be-

tween them. The posterior foramen (or two foramina) seems comparable to the foramen rotundum in other mammals. The two branches of the maxillary division unite to form the infraorbital nerve. The vidian nerve could not be separated or distinguished from these. The main trunk of the infraorbital nerve enters the infraorbital canal; inside the canal a twig, the anterior superior alveolar nerve, descends into the maxillary bone. The trunk continues out onto the side of the snout. A small medial branch, the sphenopalatine, comes off the infraorbital nerve where it enters the orbit; it re-enters the skull through the sphenopalatine foramen. As it crosses the orbital floor it gives off a descending palatine branch, which enters the dorsal palatine foramen, runs through the palatine canal, and emerges on the palate through the posterior palatine foramen.

In company with the anterior portion of the maxillary division, the ophthalmic division (1st) of the trigeminal, and the abducens (VI), trochlear (IV), and oculomotor (III) nerves enter the alisphenoid canal. The foramen through which they pass is comparable to the orbital fissure in other mammals. The nasociliary branch of the ophthalmic re-enters the skull through the more anterior of the two ethmoid foramina. The frontal branch of the ophthalmic ascends the medial wall of the orbit and exits onto the top of the skull through the supraorbital notch.

The optic nerve (II) enters the orbit through the large, oval optic foramen. It is situated entirely within the orbitosphenoid.

ARTERIES

The common carotid artery gives off three branches when it reaches the back of the larynx. The superior thyroid artery diverges medially; the stapedial and occipital arteries branch off on the lateral side. The main trunk continues as the external carotid. The occipital artery turns posteriorly and crosses ventral to the stapedial. It runs through a channel between the condyle and the paroccipital process to the back of the head and neck.

The stapedial artery in company with the vagus, accessory, and glossopharyngeal nerves passes through the jugular foramen, and it enters the stapedial foramen in the bulla. It exits from the middle ear and enters the cranial cavity via the stapedial artery canal in the periotic. A dorsal branch from it continues out the temporal foramen to the temporal muscle. The main portion runs anteriorly and exits via the sphenofrontal foramen into the orbit; this is the ophthalmic artery, which supplies the eye and eye muscles with blood. One branch, the ethmoidal artery, enters the posterodorsal ethmoid foramen. Another, the superior ophthalmic artery, ascends the medial wall of the orbit with the frontal branch of the ophthalmic nerve and goes through the supraorbital notch onto the top of the head.

The external carotid artery bends laterally and gives rise to auricular, internal maxillary, and other branches which supply the lower jaw, jaw muscles, and ear region with blood. At the bend, the external maxillary artery diverges and runs anteriorly between the masseter and digastric muscles. It gives off a lingual artery and a glandular branch. In this region a third branch proceeds dorsally, gives off a tiny meningeal twig to the foramen ovale, enters the alisphenoid canal, and passes as the internal maxillary into the orbit where it divides into three branches.

The outermost branch of the internal maxillary artery, the posterior superior alveolar, runs anterolaterally to the cheek region. The middle branch, the infraorbital, gives off minute branches that enter the nutritive foramina. It passes through the infraorbital foramen where a miniscule orbital twig pierces the bone dorsally, emerges from the malar foramen, and goes into the tissue anterior to the eye; a ventral branch, the anterior superior alveolar, in company with the nerve of the same name, enters a foramen below. The main trunk

continues out onto the snout. The innermost branch of the internal maxillary artery gives rise to the descending palatine artery and continues on into the sphenopalatine foramen. The descending palatine artery enters the dorsal palatine foramen, runs through the palatine bone, and emerges from the posterior palatine foramen; it diversifies in the tissue of the palate and disappears again into the incisive foramen.

VEINS

Three distinct trunks carry blood from various parts of the head. These are the anterior and posterior facial veins, which unite in the neck to form the external jugular vein, and the internal jugular vein.

The posterior facial receives blood from the temporal and orbital-palatine regions. The infraorbital vein begins on the snout and passes through the infraorbital canal where it picks up a small twig from the anterior alveolar foramen. In the orbit, as the internal maxillary vein, it collects twigs from the nutritive foramina and small branches from veins passing through the sphenopalatine foramen and palatine canal. The descending palatine vein ascends through the posterior maxillary notch and joins it at the back of the maxilla. There are two ethmoid foramina, and the ethmoid vein exits through the posterodorsal one. It joins the ophthalmic, which then unites with the internal maxillary just before it enters the sphenoidal fissure. The internal maxillary occupies most of the space within the alisphenoid canal, the internal maxillary artery filling only a small dorsal portion of the canal. The vein communicates through the transverse canal in the basisphenoid with the same vein on the opposite side. It empties into the pterygoid plexus.

The superficial temporal vein gathers the posterior deep temporal, transverse facial, masseteric, and auricular branches. It is joined by a large vein from the temporal foramen and condylar area. This broad vessel also continues into the pterygoid plexus. The inferior alveolar vein enters the plexus from the mandibular foramen in the jaw. The plexus anastomoses dorsally with the internal maxillary vein and ventrally with the submental vein. A meningeal branch enters it through a small foramen between the bulla and the basisphenoid bone; this aperture may be a remnant of the middle lacerate foramen. The pterygoid plexus changes from a sack-like structure into a large vein that proceeds posteriorly and is called the posterior facial vein.

The anterior facial vein begins on the snout. It gathers tributaries from the masseteric and submental regions. It passes back into the neck where it unites with the posterior facial vein to form the external jugular.

The internal jugular vein is quite small. It collects a branch from the inferior petrosal sinus in the carotid canal, leaves the cranium through the jugular foramen in company with the nerves and the stapedial artery, turns posteriorly with them, and passes into the neck.

Foramina of the Rodent Skull

I have followed, as far as possible, the terminology used by Hill (1935) and have attempted to find names commonly used in the literature for foramina he did not describe. My main points of departure from Hill are in the temporal and pterygoid regions. I have retained the term postglenoid foramen but have abandoned the names subsquamosal, postsquamosal, suprasquamosal, and squamosal in favor of the general term temporal foramina. In the Rodentia the temporal foramina are quite variable and cannot be categorized. The new terms post-alar fissure, squamoso-mastoid foramen, and foramen ovale accessorius are used for apertures that are different from anything in Hill's list. The fossils demonstrate that Hill's distinction between alisphenoid and sphenopterygoid canals is not universal in the order; only one canal, the alisphenoid, is present in the earliest rodents, and the sphenopterygoid

appears to be unique to geomyoids among the groups examined.

The following topographic list of foramina and their contents is based mainly on the woodchuck (*Marmota monax*) unless otherwise stated. I have indicated also those foramina present but not figured, because they are hidden by another structure. Foramina lacking in *Marmota* are described from the rodents in which they occur. No rodent possesses all of the foramina listed.

1. The unpaired interpremaxillary foramen does not occur in the woodchuck. When present it is situated just behind the incisors on the median premaxillary suture, and it transmits a branch of the palatine
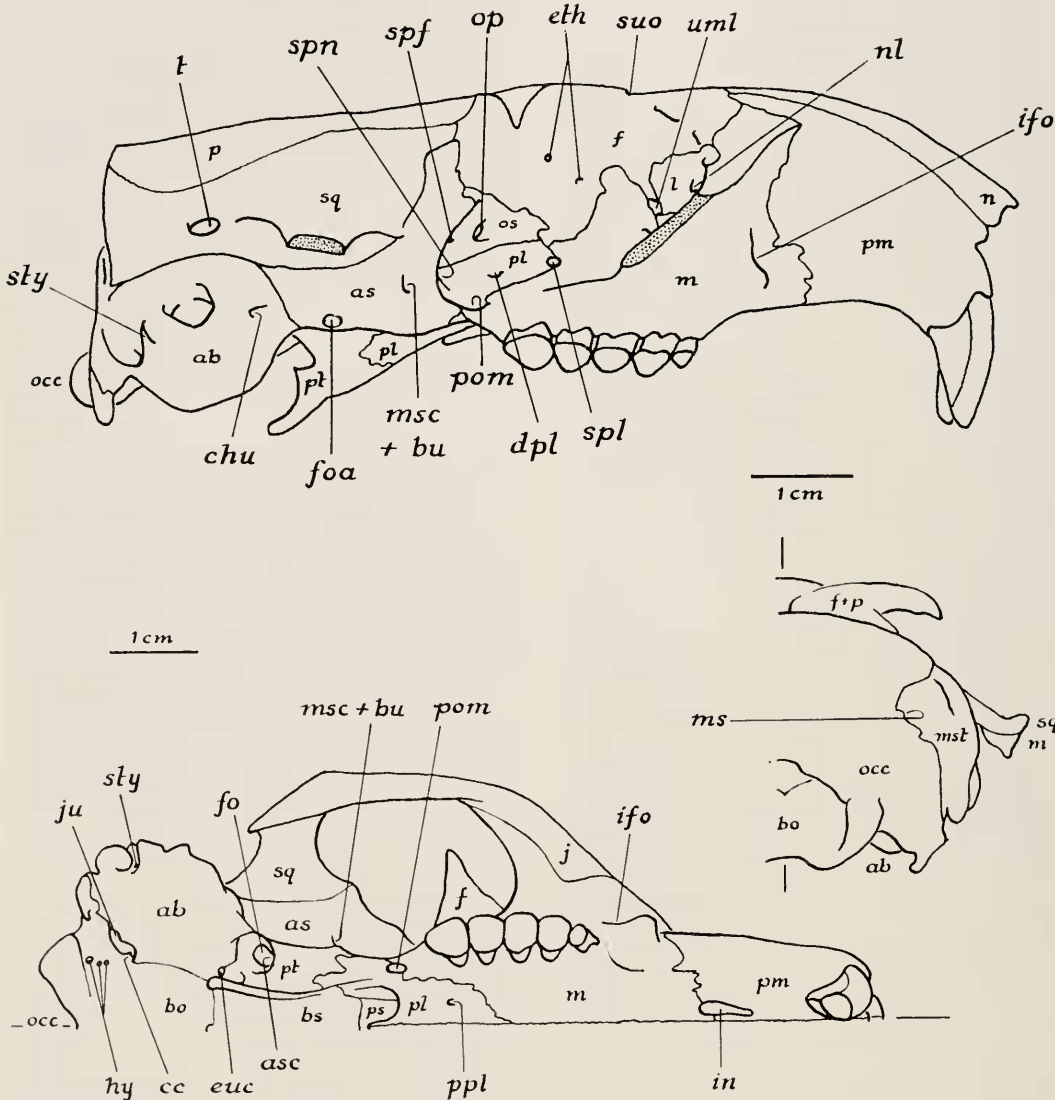

Figure 1.   *Marmota monax* (MCZ B9911).

artery. As Hill (1935:122) states, it is relatively large in *Aplodontia*.

2. The incisive foramina flank the midline of the diastema. The lateral margin of each is intersected posteriorly by the premaxillary-maxillary suture. Each transmits a duct from the nasal passage, a branch of the palatine artery, and a branch from the palatine vein.

3. The major posterior palatine foramen is usually situated in the maxillary-palatine suture. It transmits the descending palatine arteries and nerves and a small vein. In many rodents a posterior pair is present in the palatine.

4. The posterior maxillary notch is situated between the end of the maxilla and the pterygoid extension of the palatine; it transmits the descending palatine vein. In many forms the notch is enclosed as a foramen.

5. The infraorbital foramen opens on the side of the snout in the maxilla. It is the anterior opening of the infraorbital canal and transmits the infraorbital nerve, artery, and vein. Protrogomorphous rodents lack the canal.

6. The anterior alveolar foramen (not figured) occurs in the floor of the infraorbital canal and transmits the anterior superior alveolar nerve plus a small artery and vein.

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Key to figures: Foramina and related structures (numbers correspond to those in text):

aa	— anterior alveolar (6)		**ppl**	— posterior palatine (3)	
asc	— alisphenoid canal (21)		**spf**	— sphenofrontal (15)	
bu	— buccinator (24)		**spl**	— sphenopalatine (11)	
bup	— posterior aperture, buccinator nerve canal (24p)		**spn**	— sphenoidal fissure (18)	
			spt	— sphenopterygoid canal (22)	
cc	— carotid canal (30)		**sqm**	— squamoso-mastoid (39)	
cca	— anterior end, carotid canal (30a)		**st**	— stapedial (31)	
chu	— canal of Huguier (40)		**stc**	— stapedial artery canal (44)	
dpl	— dorsal palatine (16)		**sty**	— stylomastoid (37)	
euc	— Eustacian canal (29)		**suo**	— supraorbital notch (10)	
eth	— ethmoid (12)		**t**	— temporal (36)	
fac	— facial canal (43)		**trc**	— transverse canal (25)	
fco	— fenestra cochleae (41)		**uml**	— unossified area in maxillary-lachrymal suture (9)	
fo	— foramen ovale (26)				
foa	— foramen ovale accessorius (27)				
fro	— foramen rotundum (20)		Bones:		
fv	— fenestra vestibuli (42)		**ab**	— auditory bulla	
hy	— hypoglossal (33)		**as**	— alisphenoid	
ifo	— infraorbital (5)		**bo**	— basioccipital	
in	— incisive (2)		**bs**	— basisphenoid	
iom	— depression, origin of inferior oblique eye muscle		**f**	— frontal	
			j	— jugal	
ipm	— interpremaxillary (1)		**l**	— lachrymal	
ito	— interorbital (13)		**m**	— maxillary	
ju	— jugular (32)		**mst**	— mastoid	
ma	— malar (7)		**n**	— nasal	
mlf	— middle lacerate (28)		**occ**	— occipital	
mn	— meningeal		**os**	— orbitosphenoid	
ms	— mastoid (38)		**p**	— parietal	
msc	— masticatory (23)		**pet**	— petrosal	
msp	— posterior aperture, masseteric nerve canal (23p)		**pl**	— palatine	
			pm	— premaxillary	
nl	— nasolachrymal (8)		**ps**	— presphenoid	
nu	— nutritive (17)		**pt**	— pterygoid	
of	— orbital fissure (19)		**sq**	— squamosal	
op	— optic (14)		stippled areas: cut through bone		
paf	— post-alar fissure (35)		solid line: seen in specimen		
pgl	— postglenoid (34)		dashed line: probable position		
pom	— posterior maxillary notch or foramen (4)		dotted line: hypothetical position		

7. The malar foramen (not figured) is situated in the orbit where the orbital and zygomatic portions of the maxilla meet above the infraorbital foramen. It transmits the malar artery from the infraorbital canal to the tissue in front of the eye. It is rarely present; presumably the artery is usually external to the bone.

8. The nasolachrymal foramen is situated in the lachrymal bone and is bounded anteriorly by the zygomatic portion of the maxilla. It transmits the lachrymal duct.

9. An unossified area between the lachrymal bone and the orbital and zygomatic portions of the maxilla is not a foramen, but the area of origin of the inferior oblique eye muscle. It has occasionally been confused with the nasolachrymal foramen.

10. The supraorbital notch is an indentation in the supra-orbital flange of the frontal bone. It permits passage of the frontal branch of the ophthalmic nerve and the superior ophthalmic artery to the top of the head. No superior ophthalmic vein was found accompanying them; it may have been too small to see. The notch occurs in the Sciuridae, only.

11. The sphenopalatine foramen is situated at the front end of the orbital process of the palatine bone above the junction of the second and third molars. The maxilla forms the rest of its margin. It transmits the sphenopalatine nerve, artery, and vein. The bones participating in the margin of the foramen differ among rodent groups.

12. The two ethmoid foramina are entirely within the orbital lamina of the frontal bone. The anterior one faces ventrally into a shallow channel and transmits the nasociliary branch of the ophthalmic nerve. The posterior is larger and more dorsal; it transmits the ethmoid artery and vein. A single ethmoid foramen, which carries the nerve, artery, and vein, is present in the orbitosphenoid-frontal suture in most rodents.

13. A single or multiple interorbital foramen pierces the orbitosphenoid in many rodents; it is absent in *Marmota* but present in some other sciurids. In geomyids it transmits a sinusoid vein between the orbits (Hill 1935:124).

14. The optic foramen is large and is entirely within the orbitosphenoid. It transmits the optic nerve.

15. The sphenofrontal foramen is situated between the orbitosphenoid and alisphenoid. It is not quite separate from the orbital fissure in some specimens. It transmits the ophthalmic artery. The foramen is absent in many groups.

16. The dorsal palatine foramen leads into the palatine canal, which runs from the orbit downward through the palatine bone and out the posterior palatine foramen. It transmits the descending palatine artery and nerve and a small vein.

17. Many nutritive foramina (not figured) occur in the orbital surface of the maxilla above the cheek tooth roots. They transmit minute branches of nerves and arteries, and are present in all the specimens examined.

18. The sphenoidal fissure has as its outer wall the alisphenoid bone. The nerves and vessels transmitted by the orbital fissure (no. 19), the foramen rotundum (no. 20), and the alisphenoid canal (no. 21) exit from it.

19. The orbital fissure (not figured) is bounded anteriorly by the orbitosphenoid, and posterolaterally by the alisphenoid. It transmits the oculomotor, trochlear, and abducens nerves, and the ophthalmic division and part of the maxillary division of the trigeminal nerve. In most rodents the fissure is united with the foramen rotundum.

20. The foramen rotundum (not figured) is completely concealed within the alisphenoid canal. It pierces the inner wall formed by the alisphenoid and transmits the remainder of the maxillary nerve; the

zygomatic branch may have a separate foramen. The foramen rotundum and orbital fissure are united in most rodents.

21. The alisphenoid canal passes lengthwise through the alisphenoid bone. It transmits the internal maxillary artery and vein.

22. The sphenopterygoid canal is absent in *Marmota*. I have found it only in geomyoids; it leads from the pterygoid fossa to the sphenoidal fissure. It transmits the internal maxillary artery, and its walls are the area of origin of the internal pterygoid muscle.

23. The masticatory foramen is situated in the alisphenoid and is often confluent with the buccinator (no. 24). It transmits the masseteric branch of the maxillary nerve.

23p. The posterior aperture of the masseteric nerve canal (not figured) can be seen just anterior to the foramen ovale in some rodents.

24. The buccinator foramen is anteroventral to the masticatory or confluent with it. It transmits the buccinator division of the maxillary nerve.

24p. The posterior aperture of the buccinator nerve canal (not figured) can be seen in a specimen of *Paramys*; usually this canal and the masseteric share a common aperture, as in *Marmota*.

25. The single transverse canal (not figured) runs between the alisphenoid canals through the basisphenoid. It transmits a vein connecting the two internal maxillary veins.

26. The foramen ovale is situated posterolaterally in the pterygoid region. It transmits the mandibular branch of the trigeminal nerve and a minute meningeal artery.

27. I define as new the foramen ovale accessorius that is lateral to the foramen ovale and transmits the mandibular branch of the trigeminal nerve to the side of the

head. It is present in forms having a substantial lateral pterygoid flange that reaches the auditory region.

28. The middle lacerate foramen is between the pterygoid region and the anterior end of the tympanic bulla or periotic as the case may be. The foramen is absent in *Marmota*; a minute aperture in the region (not figured) transmits a meningeal vein.[1]

29. The Eustachian canal emerges dorsal to the anteromedial portion of the tympanic bulla. It transmits the Eustachian tube.

30. The carotid canal begins at or in front of the anterior end of the jugular foramen and runs anteriorly between the basioccipital and the periotic and tympanic. In many rodents having a canal it transmits the internal carotid artery. In *Marmota*, however, it transmits a vein, the inferior petrosal sinus, which joins the internal jugular vein.

30a. In some fossil rodents there is a foramen leading into the cranium anteromedial to the periotic. It seems to be the anterior end of the carotid canal.

31. The stapedial foramen (not figured) is dorsolateral to the jugular foramen and shares a common aperture with it. It enters the middle ear probably in the fused suture between the tympanic and periotic, and transmits the stapedial artery.

32. The lenticular jugular foramen is between the basioccipital and the posteromedial part of the bulla. It transmits the vagus, accessory, and glossopharyngeal nerves, the stapedial artery, and the internal jugular vein.

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[1] The function of the foramen is uncertain; no description exists of its contents in any of the Recent forms I have examined. In muroids it transmits the portion of the stapedial artery which emerges from the anterior part of the middle ear (Guthrie, 1963). In the dog the internal carotid artery passes through the foramen into the cranium (Gregory, 1910:430).

33.   The hypoglossal foramen in the basi-occipital is anterior to the condyle and may be subdivided into two or more parts. It transmits the hypoglossal nerve.

34.   The postglenoid foramen pierces the squamosal bone ventral to the zygomatic root and posteromedial to the glenoid fossa. It is absent in many *Marmota* skulls. When present, it transmits a large vein that drains most of the cranial cavity.

35.   The post-alar fissure is absent in *Marmota*. I introduce this term for an opening between the alisphenoid wing and the tympanic bulla; it probably serves a function similar to that of the postglenoid foramen. In some forms it separates a part of the squamosal from the tympanic.

36.   The temporal foramen is absent in *Marmota*. When present it is within the squamosal bone or in the squamoso-parietal suture, usually posterodorsal to the root of the zygomatic arch. It serves the same function as the postglenoid foramen and can take over the entire function of that opening. In some forms there are two or more temporal foramina.

37.   The stylomastoid foramen is between the external auditory meatus and the mastoid process. It transmits the facial nerve, and is constant in all rodents that possess a bulla.

38.   The mastoid foramen is on the occipital surface between the occipital bone and the medial portion of the mastoid bone. It transmits a small vessel which, according to Hill (1935:128), is a vein from the neck muscles to the transverse sinus.

39.   The squamoso-mastoid foramen is absent in *Marmota*. I introduce the term for the foramen, which is present in many rodents, on the occipital surface between the squamosal and the mastoid. It transmits a vein.

40.   The canal of Huguier is a minute slit in the anterior surface of the bulla. It transmits the chorda tympani division of the facial nerve.

The following, which are not, strictly speaking, cranial foramina, have been shown in figures of several early rodents. They are useful as points of reference, and the canals are, of course, associated with soft parts intimately related to cranial foramina.

41.   The fenestra cochleae (rotundum) is a round, membrane-covered aperture leading into the scala tympani of the cochlea.

42.   The fenestra vestibuli (ovale) is an oval, membrane-covered aperture leading into the scala vestibuli of the cochlea. The footplate of the stapes rests on this membrane.

43.   The facial canal is in the periotic dorsolateral to the promontorium and is the canal in which the facial nerve traverses the middle ear.

44.   The stapedial artery canal is also situated in the periotic dorsolateral to the promontorium, and is the canal by which the stapedial artery exits from the middle ear. In many of the fossils it appears to be united, in part, with the facial canal.

PARAMYIDAE

Paramys

Specimens examined:
   Paramys copei (Figs. 2 and 4): Lysite Member, Wind River Formation: PU 16564 p. Lost Cabin Member, Wind River Formation: AMNH 4755 (type) npot, 4756 potc.
   P. delicatior: Twin Buttes Member equivalent, Bridger Formation: AMNH 55675 po.
   P. delicatus (Fig. 3): Blacks Fork Member, Bridger Formation: AMNH 12506 s, 13090 s; USNM 23556 s; YPM 13381 npo.
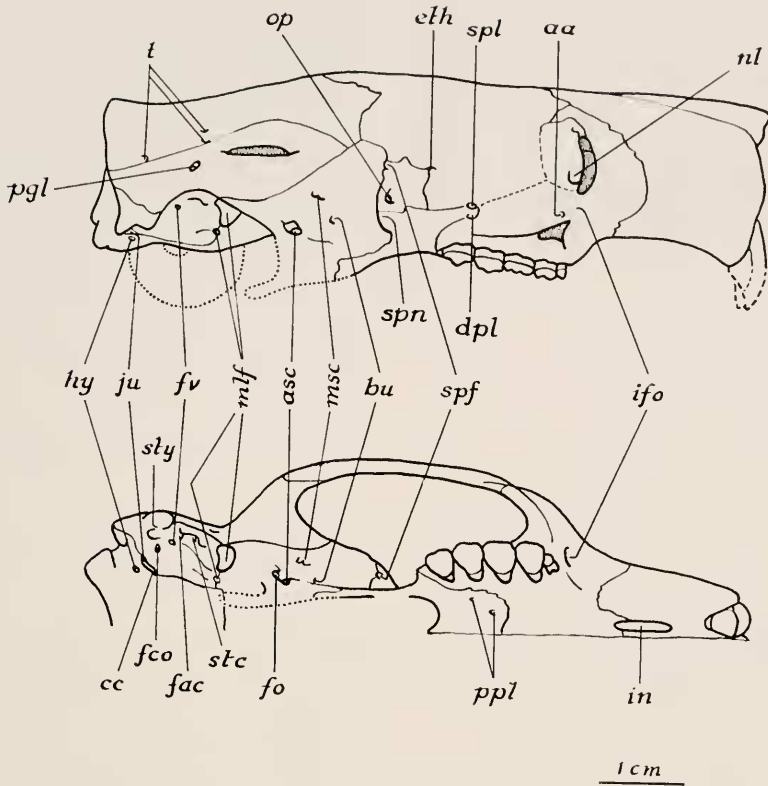   *P. sp.*: Willwood Formation: PU 17421 np.

Figure 2. *Paramys copei* (composite of AMNH 4755 and 4756). See Fig. 1 for key to foramina.

Foramina

The ratio of length of the incisive foramina to diastemal length ranges from .42 to .45. The lateral margins of the foramina are intersected behind the middle by the premaxillary-maxillary suture, which runs posterolaterally away from them.

The posterior palatine foramina are wholly within the palatine bones. The larger anterior pair is close behind the maxillary-palatine suture and medial to the posterior halves of the first molars. The smaller posterior pair is more laterally situated than the anterior and is medial to the posterior halves of the second molars. The maxilla ends behind the cheek teeth in a blunt point. There is a slight posterior maxillary notch between it and the pterygoid extension of the palatine.

In front view the infraorbital foramen is elliptical; the major axis is inclined so that the top of the foramen is farther lateral than the bottom. The axis in *P. copei* measures 3.0 mm; in *P. delicatus,* 4.0 mm. In lateral view the foramen is approximately vertical. The anterior alveolar foramen, which is in the curve formed by the orbital wall and floor, is just posterior to the infraorbital, and is directed anteromedially. In front of the infraorbital there is a small foramen, probably for the nasal branches of the infraorbital artery and nerve. This foramen is more pronounced and more ventral in *P. delicatus* than in *P. copei.*

The lachrymal region is preserved only in the type specimen of *P. copei,* AMNH 4755. The nasolachrymal foramen is dorsal
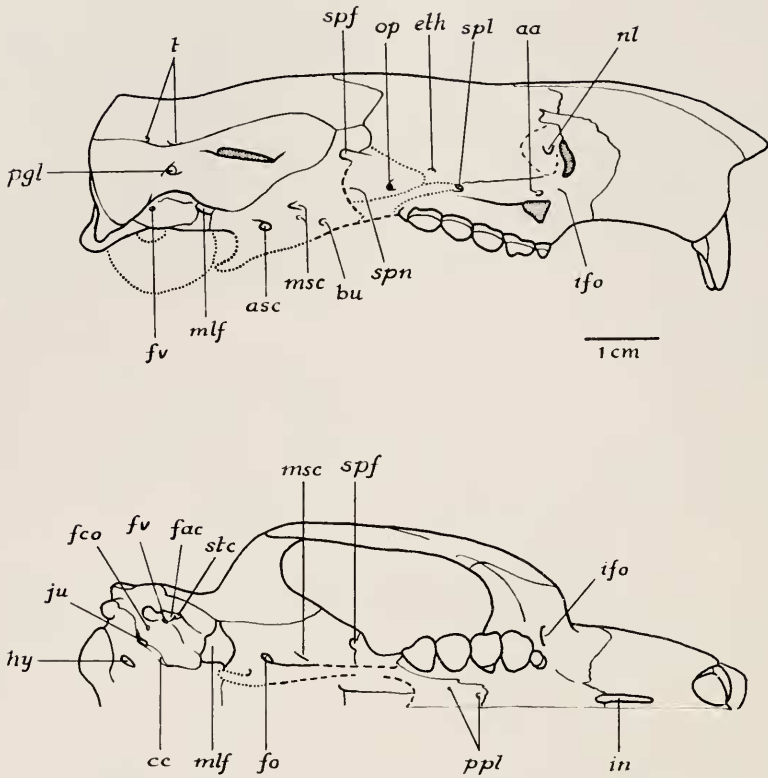
Figure 3. *Paramys delicatus* (USNM 23556). See Fig. 1 for key to foramina.

to and not far above the infraorbital, and it is below the lachrymal flange of the zygoma. A channel for the lachrymal duct descends the face of the lachrymal bone to the foramen. Sutures around the foramen are not visible.

The sphenopalatine foramen is dorsal to the junction of the second and third molars. The maxilla and orbital process of the palatine make up its borders; the frontal may reach it dorsally, but this is not clear. The orbitosphenoid is excluded from the margin. Wood (1962:15, fig. 3A) figures the sutures incorrectly and shows the foramen surrounded by the maxilla. The ethmoid foramen is dorsal and posterior to the third molar. It is within the frontal bone and is overhung by a lip from it. In the type specimen of *P. copei*, the frontal-orbitosphenoid suture reaches it posteriorly;

in *P. delicatus*, AMNH 12506, the suture does not. The optic foramen, which is within the orbitosphenoid, is nearly 1.0 mm in diameter. It is dorsal and considerably posterior to the third molar. In *P. copei* it is closer to the sphenoidal fissure than in *P. delicatus*.

The dorsal palatine foramen, which is in the maxillary-palatine suture, is immediately ventral to the sphenopalatine, and both are within a single depression. Three specimens, AMNH 4755, 12506, and 55675, show this condition clearly. The same occurs in *Thisbemys corrugatus*, AMNH 94008 (for which there is no locality data; this is the only detail known of the foramina of *Thisbemys*, so I include it here). Minute nutritive foramina are present, as in all rodents, in the floor of the orbit above the roots of the cheek teeth.

The sphenoidal fissure at its opening is separated from the cranial cavity by a wall of bone; it is situated well behind the cheek teeth. In *P. delicatus* a slight ridge sets off the dorsal portion as a distinct channel. The alisphenoid canal joins the sphenoidal fissure laterally.

The prominent sphenofrontal foramen is in the orbitosphenoid-alisphenoid suture near its junction with the frontal. In *P. delicatus*, USNM 23556, a conspicuous channel leads gradually downward and forward from the foramen. Wood (1962: 15, fig. 3A) has labeled a puncture in the bone as the sphenofrontal foramen; actually, it is indicated in his figure by a dark area 2 mm behind and 3 mm above the point he has labeled.

The masticatory and buccinator foramina are separate, the distance between them ranging from 1.0 to 3.0 mm. They face anterodorsally and anteriorly, respectively, and are a minimum of 3 mm from the foramen ovale. A minute foramen occurs between them in *P. delicatus* but not in *P. copei;* this was possibly for a branch that split off the masseteric nerve before it emerged from the masticatory foramen. The buccinator foramen is farther anterior with respect to the masticatory in *P. delicatus.* Wood (1962:15, fig. 3) has interpreted these foramina differently and, I believe, incorrectly.

The pterygoid region of *P. copei* is bounded medially by a flange and laterally by a faint ridge that is sufficient to enclose a foramen ovale accessorius. Medial to the foramen there is an oval depression. Within it are four foramina (Fig. 4). The posterior one leads from the braincase and is clearly the foramen ovale. The medial foramen leads into two canals; one, anteriorly directed, is the alisphenoid; the other, medially directed, is the transverse canal. The anterior and lateral foramina lead to the buccinator and masseteric nerve canals respectively. I am in agreement with Black (1968a:291, fig. 18) as regards their interpretation. In *P. delicatus* the lateral ptery-
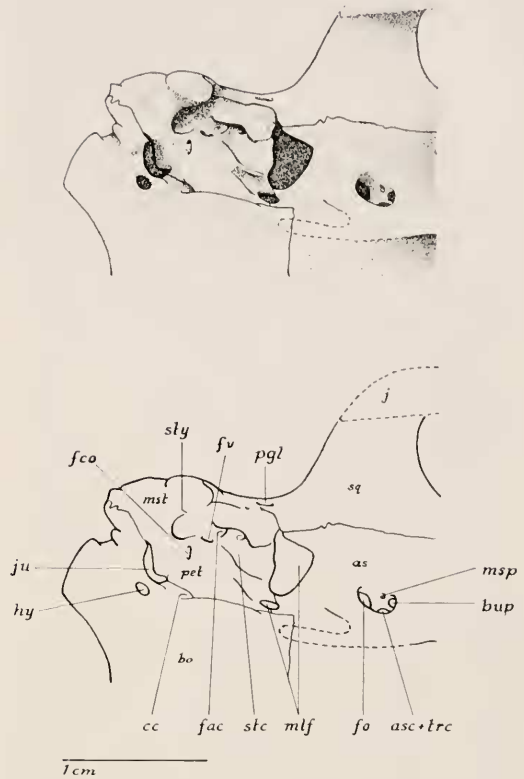

Figure 4. Auditory and pterygoid regions of *Paramys copei* (AMNH 4756). Labeled outline drawing (hamular process hypothetical), and shaded drawing of the same. See Fig. 1 for key to foramina.

goid ridge is somewhat weaker. A single large foramen, the foramen ovale, is visible in ventral view; in one specimen, AMNH 12506, a small foramen, probably the transverse canal, opens in its anteromedial wall.

The tympanic bones are absent in all specimens of *Paramys,* and the middle lacerate foramen is completely exposed. In *P. delicatus* it seems to be a single, irregular opening. In *P. copei* a strut of bone transforms the medial portion into a separate, oval-shaped foramen. Wood (1962:42) interprets this latter as the entire middle lacerate foramen and states that the larger lateral part is apparently the foramen ovale. Since the specimen has a readily identifi-

able foramen ovale in the usual position, Wood's designation cannot be correct. Black (1968a:291, fig. 18) has identified the foramina as I do; the smaller medial one he identifies as a part of the carotid canal.

The carotid canal begins at the anterior end of the jugular foramen, it was probably open ventrally, and presumably transmitted a branch of the internal carotid artery. The canal may emerge from between the basi-occipital and the petrous portion of the periotic and enter the cranium through the medial portion of the middle lacerate foramen, but this cannot be determined with certainty. The jugular foramen, as in all rodents, is lenticular in shape and is situated between the periotic and basioccipital. The hypoglossal foramen is single in *P. copei* and *P. delicatus*. The posterior of two hypoglossal foramina shown by Wood (1962:15, fig. 3E) is a break in the bone.

The postglenoid foramen, which is behind the glenoid fossa below the zygomatic root, is in the squamosal bone. Its major axis is smaller in *P. copei* than in *P. delicatus*, about 1.5 and 2.5 to 3.5 mm respectively. Temporal foramina are concentrated in the squamoso-parietal suture. Antero-dorsal to the postglenoid is a single foramen in the suture. In some specimens it is accompanied by a second opening either above in the parietal (AMNH 4756, right side; AMNH 12506, left side) or below in the squamosal (USNM 23556, left side). A smaller foramen, also situated in the suture, is about halfway between these foramina and the back of the parietal.

A mastoid foramen is present in the mastoid-occipital suture. It is well above the level of the top of the foramen magnum. The foramina within the auditory region are exposed because the tympanic was not attached and has been lost. The least distorted periotic is preserved in a specimen of *P. copei*, AMNH 4756. The major features of the auditory region are shown in Figure 4. Wood (1962:43, fig. 14A) and Black (1968a:291, fig. 18) figure the same portion of this specimen. The most complete description of a paramyid periotic is given for *P. delicatus* by Wood (1962:15, fig. 3B and C; page 18).

A lateral shelf of the periotic begins at the middle lacerate foramen and continues posteriorly for two-thirds of the length of the petrous portion. Behind it the mastoid portion broadens, curves medially to the posterior end of the jugular foramen, and ascends the occipital surface; most of this region is exposed outside the middle ear. Lateral to the fossa for the stapedius muscle there is a protuberance of the mastoid that is not situated so far posteriorly as the mastoid process in later rodents.

Medial to the lateral shelf a broad channel, which narrows posteriorly, runs from the middle lacerate foramen to the fossa for the stapedius muscle. In the absence of a tympanic the stylomastoid foramen is simply a groove lateral to the fossa on the medial surface of the mastoid protuberance and not a foramen as indicated in Wood's figure. The anterior part of the channel is presumably the area of origin of the tensor tympani muscle. In the middle portion are two posteriorly facing foramina, which are just internal to the shelf. The anterior one appears to be the foramen through which the stapedial artery left the middle ear; the posterior one, the foramen through which the facial nerve entered the middle ear.

The medial portion of the auditory region is occupied by the promontorium. A faint channel, which marks the course of the stapedial artery, runs from the fenestra vestibuli to the anterior end of the jugular foramen. This portion of the channel corresponds in position to the indentation for the stapedial foramen in the bulla of *Reithroparamys* (Fig. 5). The fenestra cochleae is in the posterior surface of the promontorium.

I do not see, as Wood did (1962:18), evidence for the position of the auditory bulla. He states that the ridge paralleling

the median margin of the petrosal and overhanging the petrosal-basioccipital suture (in AMNH 12506) seems to have served for bracing the median wall of the bulla. But the particular specimen he described is distorted; the petrosal has been tipped and the basioccipital crushed so that this ridge, which originally abutted against the basioccipital, now stands away from it. The ridge in its proper position could not have braced the bulla.

Wood also states that the depression between the mastoid region and the lateral shelf of the periotic " . . . seems to have held the meatal tube of the bulla" (p. 18). It is more likely, however, that the meatus was lower down, as in *Reithroparamys* (Fig. 5) and *Sciuravus* (Fig. 7) and that the depression contained the dorsal portion of the tympanic.

Leptotomus

Specimens examined:
> *Leptotomus bridgerensis*: Twin Buttes Member, Bridger Formation: AMNH 12507 t.
> *L. costilloi*: Huerfano Formation: AMNH 55110 s, 55111 (type) s.
> *L. parvus*: Twin Buttes Member, Bridger Formation: AMNH 12519 (type) p, 93030 p.

FORAMINA

Although two of these specimens are complete skulls, they are so fractured and crushed that very little information can be gotten from them.

The two partial palates of *L. parvus* show that the posterior palatine foramina are wholly within the palatine bones, close behind the maxillary-palatine suture. The large pair is medial to the anterior part of the second molars. These are connected, each by a canal through the bone, to their respective dorsal palatine foramen. The latter is situated in the maxillary-palatine suture immediately ventral to the sphenopalatine foramen and above the anteriormost part of the third molar.

In lateral view the infraorbital foramen is vertical; its exact shape and disposition cannot be determined.

The sphenoidal fissure at its opening is separated from the cranial cavity by a wall of bone. It is well behind the last molar. Details of the region are visible in the fragmentary specimen of *L. bridgerensis*. A slight ridge sets off the dorsal portion as a distinct channel. The alisphenoid joins the fissure laterally. A foramen in the medial wall of the alisphenoid canal is probably the entrance to the transverse canal; it would be completely hidden in an unbroken specimen. The exposed channel through the bone to the sphenofrontal foramen is large and runs anteroventrally to a position that was probably very close to the top of the sphenoidal fissure.

The pterygoid region is partially preserved in AMNH 55110. The foramen ovale is large, and the lateral pterygoid flange bridges it ventrally to form a foramen ovale accessorius.

The carotid canal appears to be like that of *Paramys;* it was probably open ventrally with the lateral lip of the basioccipital shielding the artery. Whether it carried the artery, or just the inferior petrosal sinus, however, cannot be determined.

The postglenoid foramen is in the squamosal under the root of the zygoma. Its major axis measures about 1.8 mm.

The auditory region is poorly preserved, but important details can be seen in the type of *L. costilloi*. The channel for the stapedial artery crosses the promontorium laterally to the fenestra vestibuli as in *Paramys*. At a point about a third of the way along its course another channel about half as wide diverges anterolaterally. Within a short distance this channel subdivides. The diverging branch runs anteromedially across the promontorium. This bifurcating channel, I believe, marks the course of the promontory artery.
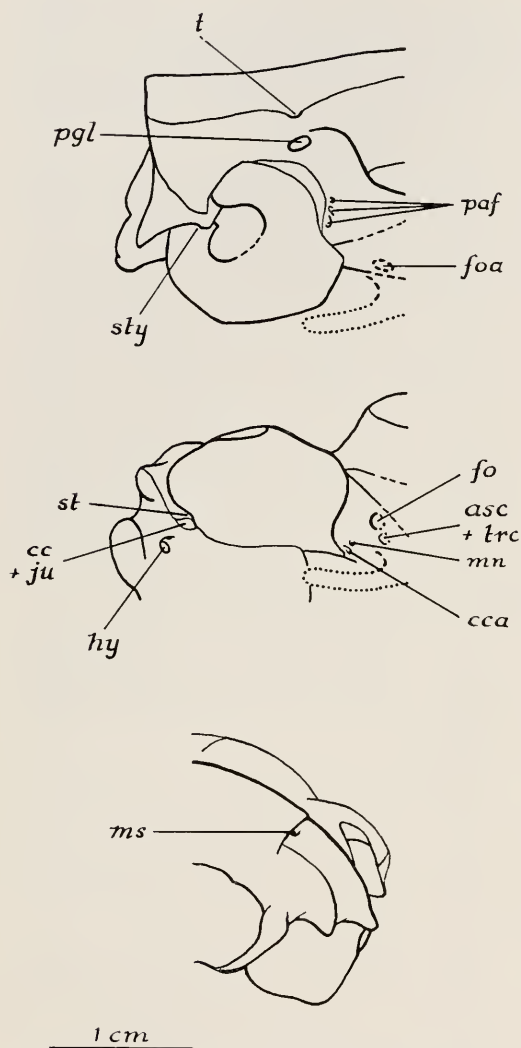
Figure 5. *Reithroparamys delicatissimus* (AMNH 12561). See Fig. 1 for key to foramina.

Reithroparamys

Specimens examined:

Reithroparamys delicatissimus (Fig. 5): Blacks Fork Member, Bridger Formation: AMNH 12561 (type) npc.

FORAMINA

The ratio of length of the incisive foramina to diastemal length is .48. The lateral margins of the foramina are intersected very near the back by the premaxillary-maxillary suture, which runs posterolaterally away from them.

A single pair of posterior palatine foramina is present within the palatine bones. It is situated far laterally, almost on the maxillary-palatine suture, and is medial to the anterior ends of the second molars. The maxilla ends behind the cheek teeth in a blunt point. There is a slight posterior maxillary notch between it and the pterygoid extension of the palatine.

In front view, the infraorbital foramen is elliptical. The major axis, which measures 3.5 mm, is inclined so that the top of the foramen is farther lateral than the bottom. In side view the foramen is approximately vertical. The anterior alveolar foramen, which is in the curve made by the orbital floor and wall, is just behind the infraorbital foramen.

The wall of the orbit and the alisphenoid bone are missing. Enough of the nasolachrymal canal is present to show that the nasolachrymal foramen was dorsal and close to the infraorbital.

The pterygoid region (Fig. 5) is mostly missing. Several details can be made out, however. The external pterygoid flange, homologous to the lateral ridge in *Paramys,* is substantial and seems to enclose a foramen ovale accessorius. Medial to the flange, the back of the foramen ovale is preserved; a channel, which is most likely the entrance to the alisphenoid and transverse canals, leads anteromedially from the foramen ovale. The middle lacerate foramen is completely covered by the auditory bulla. Just anterior to the bulla and lateral to the styloid process are two elongate foramina. A channel extends posteriorly under the bulla from the medial one. This suggests that the foramen may have been an aperture for a branch of the internal carotid artery, possibly the promontorial. The Eustachian canal passes over it. The lateral foramen may have transmitted a meningeal vessel.

The carotid canal appears to begin at the

anterior end of the jugular foramen and does not have a distinct entrance. A shelf of the periotic is exposed anterolateral to the jugular foramen at the point where the bulla is indented. The stapedial foramen is in this indentation and between the tympanic and periotic. The hypoglossal foramen is double on both sides. The larger foramen opens ventrally and faces anterolaterally; its rim continues out toward the jugular foramen. The second foramen is under the rim of the larger and opens and faces anteromedially.

The postglenoid foramen is within the squamosal bone. Its major axis is 2.1 mm long. On the left side of the skull are three foramina in front of the periotic, which is sandwiched between the bulla and squamosal. These foramina may be homologous with the post-alar fissure of some later sciuromorphous forms. A large temporal foramen is present in the squamoso-parietal suture above the postglenoid. There seems to be a much smaller one, behind it, also in the suture.

The stylomastoid foramen is bounded by the bulla and mastoid element. There is a short protuberance of the mastoid lateral to it. The mastoid foramen is above the level of the top of the foramen magnum and is in the mastoid-occipital suture.

Ischyrotomus

Specimens examined:

> *Ischyrotomus oweni*: Blacks Fork Member, Bridger Formation: USNM 17161 s; 17160 (type) s (specimen not available to me; information taken from Wood, 1962).
>
> *I. horribilis*: Blacks Fork Member, Bridger Formation: USNM 17159 (type) s.
>
> *I. petersoni*: Myton Member, Uinta Formation: AMNH 2018 (type) s.

FORAMINA

The ratio of length of the incisive foramina to diastemal length ranges from .18 to .21. The lateral margins of the foramina are intersected near the back by the premaxillary-maxillary suture, which runs posterolaterally away from them.

The pair of larger posterior palatine foramina is in the maxillary-palatine suture and is medial to the middle region of the first molars. The smaller posterior pair, entirely within the palatine, is in line with the larger pair and medial to the anterior halves of the second molars. In *I. oweni*, USNM 17161, there are two minute foramina situated more laterally in the palatine. The maxilla ends behind the cheek teeth in a distinct point that is best seen in *I. horribilis*. There is a posterior maxillary notch between it and the pterygoid extension of the palatine.

In front view, the infraorbital foramen is elliptical, and the major axis is inclined so that the top of the foramen is farther lateral than the bottom. The axis in *I. horribilis* is 3.3 mm long; in *I. oweni*, 4.4 mm; in *I. petersoni*, 4.5 mm. In side view the foramen is approximately vertical. The lachrymal region in these specimens is either missing or damaged. Wood (1962: 189) reports that the nasolachrymal foramen is between the lachrymal and maxillary bones in the medial wall of the orbit.

Wood (1962:189–190) states, "The sphenopalatine foramen sometimes lies on the frontal-maxillary suture and sometimes in the maxilla as in *Paramys*. It is a little farther to the rear, just behind M³ instead of just in front of it." His interpretation of its position in *Paramys* is incorrect, as noted above, and his placement of it in *Ischyrotomus* also seems erroneous. Wood (1962: 207, fig. 71), in his figure of USNM 17160, shows the foramen within the maxilla and dorsal to the back of the second molar. Its position cannot be determined in the other specimens. The ethmoid foramen is above and between the sphenopalatine and optic foramina. A slight lip of bone overhangs it. Sutures in this region are indeterminate. The optic foramen, which is about 1.0 mm in diameter, is dorsal and considerably
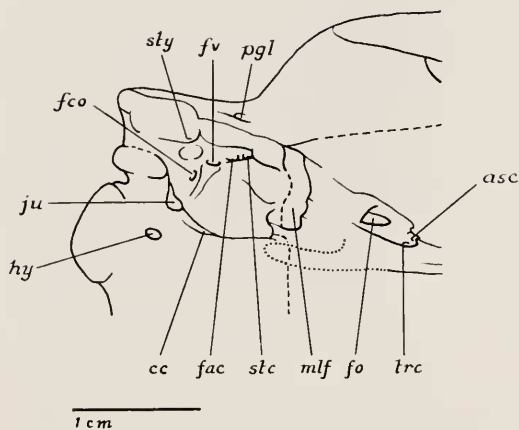
Figure 6.   Auditory and pterygoid regions of *Ischyroto-mus oweni* (USNM 17161). See Fig. 1 for key to foramina.

posterior to the third molar, and it is near the sphenoidal fissure.

The dorsal palatine foramen was not seen; the region in which it would occur is fractured in every specimen. The sphenoidal fissure at its opening is separated from the cranial cavity by a wall of bone. A low ridge sets off its dorsal portion as a distinct channel. The alisphenoid canal unites with the fissure. The sphenofrontal foramen is dorsal to the sphenoidal fissure and postero-dorsal to the optic foramen; a conspicuous channel leads downward and forward from it. Sutures in this area are indistinct in all specimens. Available specimens are too crushed in the alisphenoid region to reveal whether the masticatory and buccinator foramina were separate or united.

The pterygoid region of *Ischyrotomus* (Fig. 6) is bounded medially by a flange and laterally by a ridge; it is not developed into a fossa and is occupied almost entirely by a depression in which there are two openings. Posterolaterally the foramen ovale opens from the cranium; the lateral ridge is interrupted alongside it, and the beginning of a foramen ovale accessorius is suggested by the hook-like termination of the ridge. Anterior and medial to the foramen ovale is the second opening; it is

deep within the angle formed where the lateral ridge and internal pterygoid flange meet. The alisphenoid canal runs anteriorly from it, the transverse canal medially. The dorsal portion of the alisphenoid canal is slightly damaged, but one small foramen, which probably transmitted the buccinator nerve, is clearly visible in its wall. The middle lacerate foramen is distorted by crushing in all specimens.

The carotid canal begins at the anterior end of the jugular foramen. The hypoglossal foramen is either single or double; when double, the apertures open into a single pit.

The postglenoid foramen is wholly within the squamosal bone. The major axis measures 1.5 mm in *I. horribilis* and 2.7 mm in *I. oweni*. Temporal foramina are in the vicinity of the squamoso-parietal suture. The largest foramen is dorsal to the post-glenoid and above the zygomatic root; in some specimens it is entirely within the squamosal; in others on the suture. There is a small foramen anterior to it and another posterior in the parietal. The occipital surface is damaged, and sutures near the mastoid foramen cannot be distinguished.

The major features of the auditory region (Fig. 6) are essentially as in *Paramys*, but there are differences in detail. The mastoid portion of the periotic has a descending process lateral and posterior to the fossa for the stapedius muscle. This mastoid process is essentially modern in aspect. The foramina in the petrosal for the stapedial artery and for the facial nerve bear the same relationship to each other as in *Paramys*. In ventral view, however, they are hidden under a single shelf which runs anterolaterally from a point on a level with the front of the fenestra vestibuli to a point overhung by the lateral shelf of the periotic. There is a distinct channel for the stapedial artery which crosses the promontorium. It is broadest at the fenestra vestibuli and narrows somewhat near the anterior end of the jugular foramen. This portion corresponds in position to the in-

dentation for the stapedial foramen in the bulla of *Reithroparamys* (Fig. 5) and *Sciuravus* (Fig. 7).

Pseudotomus

Specimens examined:
> *Pseudotomus hians*: ?Blacks Fork Member, Bridger Formation: AMNH 5025 (type) nptc.

Foramina

A portion of the external margin of the right incisive foramen is present. Its curvature suggests that the foramen was relatively short, as in *Ischyrotomus*.

At the back of the maxilla, near the middle of the palate, a slight channel leads posterodorsally into what was probably the larger of the posterior palatine foramina. It was evidently medial to the middle of the first molar and in the maxillary-palatine suture.

The infraorbital foramen is broad and elliptical. The major axis, which measures 3.5 mm, is inclined so that in front view the top of the foramen is farther lateral than the bottom, and in side view the top is slightly farther anterior than the bottom. The anterior alveolar foramen, which is in the curve made by the orbital floor and wall, is just behind the infraorbital. The nasolachrymal foramen is dorsal to and not far above the infraorbital and is below the posterior protuberance of the lachrymal bone. A wide channel descends the surface of the lachrymal and bends anteriorly into the foramen. The maxilla appears to form the ventral margin of the foramen.

Both orbits are considerably damaged and the fragments of bone displaced; sphenopalatine and dorsal palatine foramina cannot be seen. The anterior part of the ethmoid foramen is preserved on the right side; a lip from the frontal overhangs it. The optic foramen, about 1.0 mm in diameter, seems to have been dorsal and considerably posterior to the last molar.

The sphenoidal fissure at its opening seems to be separated from the cranial cavity by a wall of bone. The sphenofrontal foramen is visible on the right side of this specimen just dorsal to the sphenoidal fissure. I do not see a channel leading from it.

The masticatory and buccinator foramina are separate and over 4.0 mm anterior to the foramen ovale. A broad channel leads dorsally from the masticatory foramen. The buccinator foramen opens anteriorly; it is directly under the middle of the masticatory and less than 1.0 mm away from it.

The pterygoid portion of *Pseudotomus* is similar to that of *Ischyrotomus*. The foramen ovale has only a hint of a lateral pterygoid ridge alongside it; there is no suggestion of a foramen ovale accessorius. The anterior portion of the pterygoid depression leads into the alisphenoid and transverse canals. A posterior projection from the anterior margin of the middle lacerate foramen indicates that the foramen was partially differentiated into medial and lateral portions. The posterior margin is not preserved.

The bullae are missing. The left periotic and the anterior end of the right are gone, and the portion of the basioccipital that normally abuts the periotic is exposed. The ventral surface of the basioccipital extends laterally as a flange that would have overlapped the anterior extremity of the periotic. Dorsal to the flange on the lateral surface of the basioccipital, there is a channel that turns up toward the cranium just behind the middle lacerate foramen; possibly this is the carotid canal, or the course of the inferior petrosal sinus. The area of the basioccipital contained within the curve of the channel is sculptured and was most likely the place where the periotic attached. The posterior part of the basioccipital is missing.

The postglenoid foramen is within the squamosal bone. Temporal foramina are present in or near the squamoso-parietal suture, but their number and exact positions are indeterminate. The mastoid foramen is above the level of the top of the

foramen magnum in the mastoid-occipital suture.

Manitsha

Specimens examined:

Manitsha tanka: Chadron Formation[1]: AMNH 39081 (type) np.

FORAMINA

The ratio of length of the incisive foramina to diastemal length is .23. The lateral margins of the foramina are not intersected by the premaxillary-maxillary suture, and it crosses the diastema behind them. The maxilla ends behind the cheek teeth in a point appressed to the palatine; there is no posterior maxillary notch.

The infraorbital foramen seems small relative to the skull size. In side view it is approximately vertical. A single hypoglossal foramen is preserved on the left side.

Discussion of the Paramyidae

The paramyid rodents form a unified group with respect to cranial foramina. There are some differences between genera and species, among which changes in the pterygoid region and various patterns of arterial channels in the auditory region are the most striking.

The ratio of length of the incisive foramina to diastemal length is high in *Paramys* and *Reithroparamys*, .42 to .48, and low in *Ischyrotomus, Pseudotomus,* and *Manitsha,* .18 to .23. The lateral margins of the foramina are intersected behind the midpoint, but not at the very back, by the premaxillary-maxillary suture. In *Manitsha* the suture crosses the diastema behind the foramina and does not run into their margins.

The posterior palatine foramina are wholly within the palatine bone in *Paramys, Leptotomus,* and *Reithroparamys.* In *Ischyrotomus* they are in the maxillary-palatine suture. A posterior maxillary notch is present in all except *Manitsha.*

In *Paramys, Thisbemys,* and *Leptotomus* the dorsal palatine foramen is associated with, but separate from, the sphenopalatine foramen; its position is uncertain in the other genera owing to crushing in the orbital region. The sphenofrontal foramen is present in *Paramys, Leptotomus, Ischyrotomus,* and *Pseudotomus.* Other skulls were too damaged for it to be found. The presence of this foramen indicates that the ophthalmic artery was a branch of either the stapedial or the internal carotid artery.

Masticatory and buccinator foramina are separate from each other and not especially close to the foramen ovale. I do not expect that *Ischyrotomus* will prove to be an exception when adequate material is found. Foramina in the vicinity of the foramen ovale differ among genera and even among species. The pattern found in *Paramys copei* could be that from which later arrangements were derived. In this species the foramen ovale, masseteric nerve canal, buccinator nerve canal, and alisphenoid and transverse canals open into a single depression. In *Ischyrotomus* and *Pseudotomus* entrances to the masseteric and buccinator nerve canals are hidden, and the depression is differentiated into two parts, one for the foramen ovale and another for the alisphenoid and transverse canals. The transverse canal was hidden in *Leptotomus* and a foramen ovale accessorius may have been present. The only available specimen of *Reithroparamys* appears to have been similar to *Ischyrotomus.* In *Paramys delicatus* the alisphenoid canal is hidden, and the foramen ovale is the only conspicuous opening in the region; the transverse canal is small but visible in one specimen and hidden in the other.

The middle lacerate foramen, when present and undistorted, appears to be

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[1] The American Museum catalogue incorrectly gives the horizon and locality for this specimen as Lower Brule, North Point of Slim Buttes, and this misinformation has been perpetuated in the literature. The correct data, supplied by M. F. Skinner (personal communication), are as follows: Chadron Formation, west side of Reva Pass, Harding County, South Dakota.
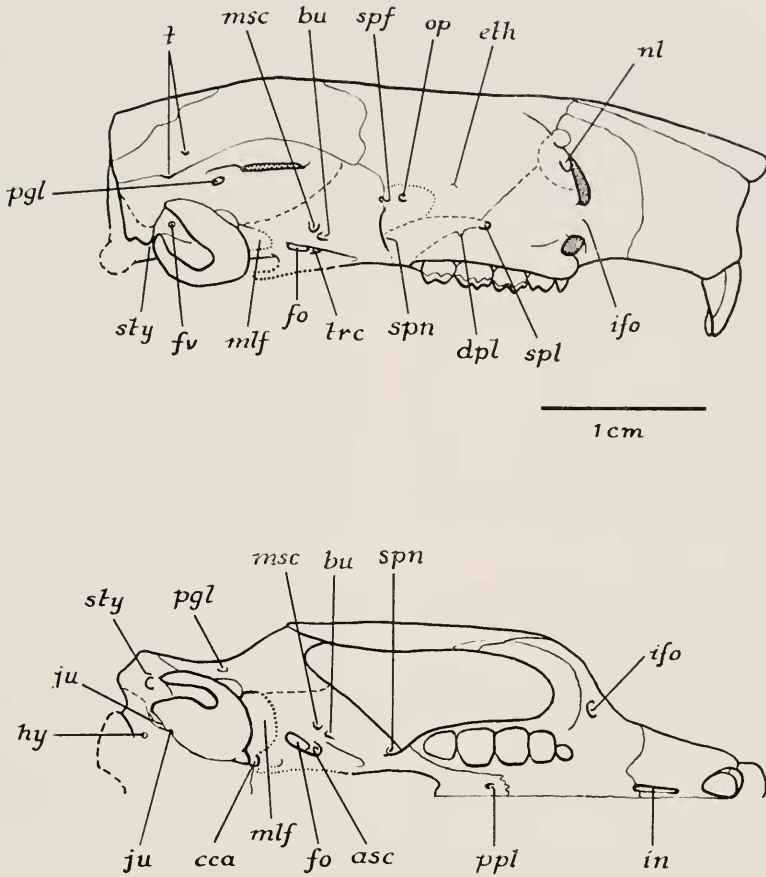
Figure 7. *Sciuravus nitidus* (reconstructed from USNM 17683, 18100, and 22477). See Fig. 1 for key to foramina.

divided into two parts, the small medial one possibly for passage of the internal carotid artery. In *Reithroparamys,* only this small aperture is visible; the tympanic bulla covers the middle lacerate foramen if it is present.

In the auditory region of *Paramys* and *Ischyrotomus* there is a channel for the stapedial artery which crosses the promontorium, and a stapedial foramen is present in *Reithroparamys.* In *Paramys* and *Ischyrotomus* there is no channel indicating the presence of the promontorial artery, whereas in *Leptotomus* this channel is clearly marked. The hypoglossal foramen is single in *Paramys,* single or double in *Ischyrotomus,* and double in *Reithro-*

paramys. A rudimentary post-alar fissure is present in *Reithroparamys* and absent in the other genera.

SCIURAVIDAE

Specimens examined:

Sciuravus nitidus (Fig. 7): Blacks Fork Member, Bridger Formation: AMNH 12531 n, 12551 nptc, 13101 npoc; USNM 17683 c, 17697 np, 17700 np, 18023 np, 18100 s, 22477 s; CM 9683 np; YPM 13458 p.

FORAMINA

Accurate measurement of the incisive foramina is possible in three specimens. The ratios of their lengths to diastemal

lengths are .41, .45, and .47. The lateral margins of the foramina are intersected near the back by the premaxillary-maxillary suture, which runs posterolaterally away from them.

The posterior palatine foramina are within the palatine bones. The large anterior pair is close behind the maxillary-palatine suture and medial to the junction of the first and second molars in some specimens, medial to the second molars in others. The smaller posterior pair is somewhat more lateral in position than the anterior and is medial to the junction of the second and third molars. The maxilla ends behind the cheek teeth in a blunt point. There is a slight posterior maxillary notch between it and the pterygoid extension of the palatine.

In front view, the infraorbital foramen is elliptical. The major axis is inclined so that the top of the foramen is farther lateral than the bottom. The axis ranges in five specimens from 1.7 to 2.6 mm. In side view the foramen is approximately vertical. The anterior alveolar foramen is just behind the infraorbital foramen in the curve made by the orbital wall and floor, and plunges anteromedially.

The structure of the lachrymal region, although not entirely preserved in any one specimen, can be determined for the most part. The nasolachrymal foramen is well above and slightly posterior to the infraorbital. It is directly below the posterior protuberance of the lachrymal bone and may be surrounded by that bone, but sutures are not clear. A short channel leads into the nasolachrymal foramen and continues anteroventrally as a canal. The canal, exposed in AMNH 12531, passes internal to the infraorbital foramen and turns medially a short distance in front of it.

The sphenopalatine foramen is dorsal to the anterior half of the second molar. It seems to be bounded posteriorly by a long orbital process of the palatine, and on the other sides by the maxilla. The frontal may be barely excluded from its margin; the orbitosphenoid is completely excluded. The minute ethmoid foramen is in the frontal above and about halfway between the sphenopalatine and optic foramina. The orbitosphenoid does not seem to reach it. It is overhung by a slight lip from the frontal. The optic foramen is not preserved clearly in any specimen, but seems, at least in USNM 18100, to have been within the orbitosphenoid. It is posterodorsal to the third molar and near the sphenoidal fissure.

The small dorsal palatine foramen is in the floor of the orbit posterior and slightly lateral to the sphenopalatine. The suture between the palatine and maxilla dips into it. The entire course of the canal descending from it can be traced in two specimens, USNM 18100 and YPM 13458 (better seen in the latter). For a short distance the canal runs between maxilla and palatine; then it emerges and continues anteroventrally on the internal surface of the palatine as a channel open into the choanae; finally it turns anteriorly through the posterior palatine foramen.

The available specimens are too damaged to show whether the sphenoidal fissure at its opening is separated from the cranium. It is situated well behind the cheek teeth. The sphenofrontal foramen, seen in one specimen, USNM 18100, is in the orbitosphenoid-alisphenoid suture just below the point at which the suture meets the frontal. A short channel leads anteroventrally from it.

The masticatory and buccinator foramina are clearly preserved in only one specimen, USNM 18100. They are close together near the foramen ovale; channels from them lead upward and forward respectively.

The pterygoid region is a relatively flat triangular surface bounded medially by a flange and laterally by a ridge; it is not developed into a fossa. There is an elongated depression medial and parallel to the posterior half of the lateral ridge. The foramen ovale opens from the cranial cavity into the posterior part of this depression. The alisphenoid canal runs forward from

the depression, and a lateral canal branches off from it to lead toward the masticatory and buccinator foramina. Medial to the alisphenoid canal is the opening into the transverse canal. Details of this region are clear in two specimens, USNM 18100 and 22477. Dawson (1961:10, plate 11) figured a distorted specimen and did not restore structures to their original positions; her sphenopalatine canal is my alisphenoid canal.

In specimens lacking the auditory bulla, the middle lacerate foramen is exposed. Its exact shape cannot be determined from the material available, but the medial portion is partially separated from the large lateral part. The medial portion is in the basi-sphenoid-basioccipital suture and pierces the side of the cranial floor. A channel leads posteriorly from the aperture across the anterior shelf of the periotic onto the promontorium. At the anterior end of the jugular foramen there is no space between the periotic and basioccipital for a carotid canal, and there is no separate entrance to a carotid canal elsewhere. The hypoglossal foramen is single.

The postglenoid foramen is within the squamosal bone. Temporal foramina can be seen clearly in USNM 18100. The largest is in the squamoso-parietal suture about halfway between the back of the zygomatic root and the posterior margin of the skull. A second small foramen is immediately behind it in the suture, and there is a small foramen in the parietal anterodorsal to these.

In most specimens the auditory bullae are missing; the periotic (Fig. 8) is clearly displayed in three specimens, USNM 18100 and 22477, and AMNH 13101. The major features are similar to those described for *Paramys*, but there are differences in relative proportions. The fenestra vestibuli, the fenestra cochleae, and the fossa for the stapedius muscle, indicated by a depression, are as in *Paramys*. A channel leads anteriorly from the stylomastoid foramen to a single foramen that is slightly anterior
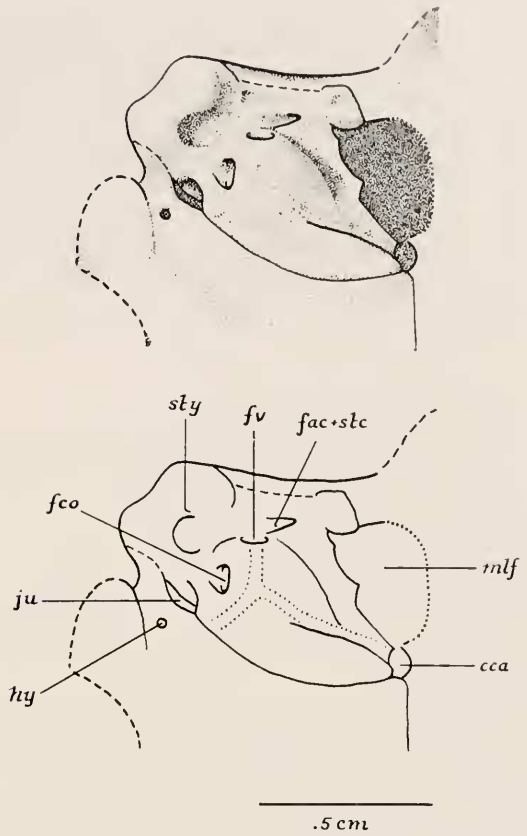

Figure 8. Auditory region of *Sciuravus nitidus* (restored from USNM 17683). See Fig. 1 for key to foramina.

to the fenestra vestibuli; the facial nerve and the stapedial artery evidently shared this one opening. Channels showing the courses of blood vessels are present on the surface of the promontorium. The main channel for the internal cartoid artery, possibly the promontory branch, begins just anterior to the jugular foramen; midway across the promontorium it turns antero-dorsally and runs to the medial portion of the middle lacerate foramen. A channel for the stapedial artery curves postero-dorsally from the point where the internal carotid turns anteriorly, and it leads to the fenestra vestibuli.

The bulla is preserved on one specimen,

USNM 22477. It has been moved out of place, and no markings on the periotic indicate precisely where it was situated. I did not notice a stapedial foramen, but one must have been present in the margin of the bulla, as indicated in Figure 7, to permit passage of the internal carotid artery. It is not possible to see in the specimen whether the bulla completely covered the middle lacerate foramen; measurements suggest that it did not, and I have so shown it in the figure.

Discussion of the Sciuravidae

The ratio of length of the incisive foramina to diastemal length is high, as in *Paramys* and *Reithroparamys,* and is much higher than those of *Ischyrotomus* and *Manitsha.* The posterior palatine foramina are within the palatine bone, again as in *Paramys* and *Reithroparamys.* A posterior maxillary notch is present, as in most paramyids.

The orbital process of the palatine reaches the back of the sphenopalatine foramen, whereas the orbitosphenoid does not. This arrangement occurs in *Paramys.* The sphenopalatine and optic foramina are farther forward relative to the cheek teeth than those of paramyids.

In *Sciuravus* the dorsal palatine foramen clearly is separated from the sphenopalatine, a condition perhaps foreshadowed in paramyids. The sphenofrontal foramen is in the orbitosphenoid-alisphenoid suture, as in paramyids. Masticatory and buccinator foramina are present and considerably closer to the foramen ovale than they are in paramyids. The arrangement of foramina in the pterygoid region is similar only to that of *Ischyrotomus* and *Pseudotomus.*

Separation of the medial part of the middle lacerate foramen to receive a branch of the internal carotid artery occurs in paramyids. *Sciuravus,* however, does not have a carotid canal between the periotic and basioccipital. Instead, the internal carotid artery entered the middle ear and crossed the promontorium in a shallow channel before entering the cranial cavity. The carotid circulation in *Leptotomus* may be the same, though the carotid canal is also present. There is only a single aperture in the petrosal for the stapedial artery and the facial nerve to exit from the middle ear, whereas in paramyids a pair of openings is visible. The postglenoid and temporal foramina are of about equal size, as in paramyids.

ISCHYROMYIDAE

Specimens examined:

I have seen and measured so many specimens (approximately 65) that a complete list would be excessive. The specimens recorded below are only those that are nearly complete or are cited in the text.

Ischyromys douglassi: Chadron Formation equivalent: CM 1123 pot; 10966 potc.

I. typus (Fig. 9): Orella Member, Brule Formation: AMNH 694 s; FMNH, P 12747 poc; MCZ 18979 potc; YPM 12521 s; PU 11383 s. Brule Formation: USNM 15929 npc; 15933 s.

I. sp: Chadron Formation equivalent: CM 24129 c. Orella Member, Brule Formation: AMNH 38865 s; CM 9463 npoc. Brule Formation: USNM 16953 s; 175352 tc; 175354 npo; CM 9755 pt.

Titanotheriomys veterior: Chadron Formation equivalent: CM 9809 p; 10660 npot. ?Orella Member, Brule Formation: MCZ 17202 s.

T. wyomingensis: Chadron Formation equivalent: AMNH 14579 (type) npt.

T. sp.: Chadron Formation equivalent: CM 8924 npt.

Foramina

The ratio of length of the incisive foramina to diastemal length, measured in seventeen ischyromyids, ranges from .21 to .30 with a cluster of nine around .24 and a cluster of eight around .28. The three specimens of *Titanotheriomys* in which this region is preserved fall at the low end of the range. The lateral margins of the
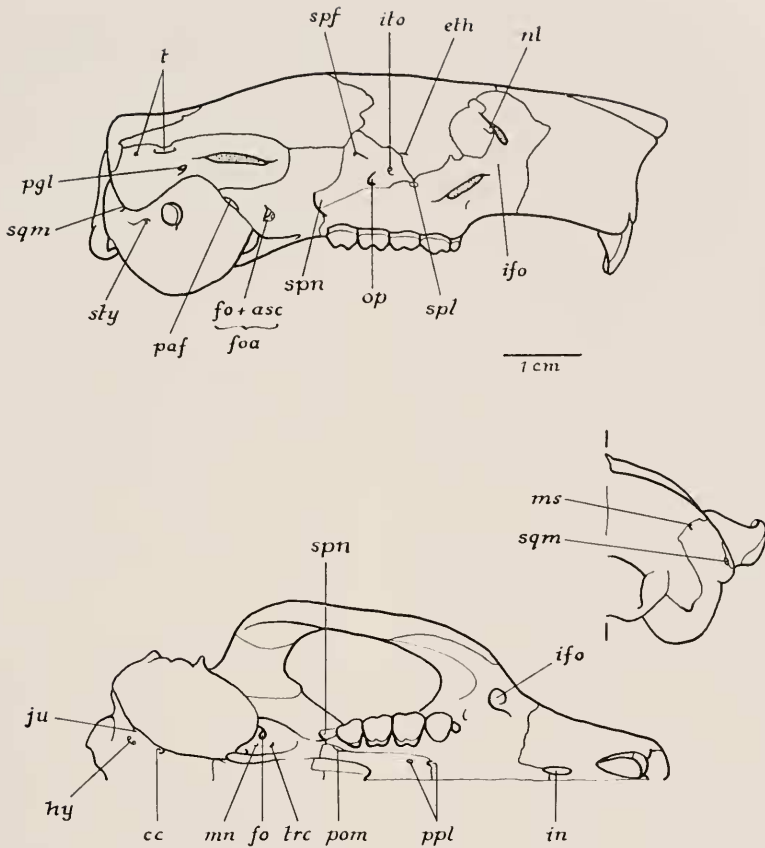
Figure 9. *Ischyromys typus* (AMNH 694). See Fig. 1 for key to foramina.

foramina are intersected at the very back by the premaxillary-maxillary suture, which runs posteriorly away from them.

The pair of larger posterior palatine foramina lies in the maxillary-palatine suture medial to an area extending from the middle of the last premolar to the middle of the first molar. The suture crosses the palate between the foramina (in one specimen, CM 9809, behind them, and a process from the palatine runs forward into the back of each foramen). There is usually a second pair of small foramina within the palatine medial to the first or second molars, and in some specimens a third pair of minute openings is present behind these. The maxilla ends behind the cheek teeth in a long point that is appressed

to the pterygoid extension of the palatine; there is a lenticular aperture between them.

In front view, the infraorbital foramen forms a pinched ellipse with the acute end ventral. The major axis has an average length of 3.6 mm and ranges from 3.0 to 4.6 mm; it is inclined so that in front view the top of the foramen is farther lateral than the bottom, and in side view the top is farther anterior than the bottom. The anterior alveolar foramen is a short distance behind the infraorbital foramen in the curve made by the orbital floor and wall, and is directed anteromedially.

The nasolachrymal foramen is dorsal to the infraorbital foramen and below the posterior protuberance of the lachrymal bone. The maxilla appears to participate

in its anterior margin. The internal course of the nasolachrymal canal can be seen clearly in one specimen of *Ischyromys*, CM 1123. A short channel descends the face of the lachrymal bone, its slight anterior inclination continuing inside the bone. It turns sharply forward near the base of the snout and proceeds anteriorly a short distance before it bends medially under the arch of the incisor. In some specimens, between the lachrymal and the orbital portion of the maxilla, there seems to be a small unossified area that is roughly horizontal and in line with the middle of the infraorbital foramen. This may mark the site of origin of the inferior oblique eye muscle, as in *Marmota*.

The sphenopalatine foramen is dorsal to the first molar. The fused maxilla and palatine surround it almost entirely, and only a very small arm of the orbitosphenoid reaches it posteriorly. The ethmoid foramen is posterodorsal to the sphenopalatine. The frontal surrounds it on three sides and a lip from the frontal overhangs it; the orbitosphenoid meets it posteriorly. In one specimen, USNM 15933, the ethmoid foramen is double. The anterior opening has the usual slit-like appearance, and a slender process from the orbitosphenoid touches it. The posterior opening is nearly round; a channel in the orbitosphenoid leads to it from behind. In this one specimen the nerve and blood vessels probably entered the bone through separate foramina, as in *Marmota*. The optic foramen, usually 1.0 mm in diameter but slightly larger in a few specimens, is within the orbitosphenoid. In most specimens it is above the posterior part of the second molar or the anterior part of the third molar; in one, CM 10966, it is above the posterior portion of the third molar.

Within the triangle formed by the optic, ethmoid, and sphenopalatine foramina is a depression in front of and closest to the optic foramen. Its deepest and most clearly defined portion is posterior. A counterpart of this depression occurs in *Marmota* in which it is the place of origin of the rectus muscles of the eye. Usually there is a small foramen in the deep part of the depression. In one fragmentary specimen, USNM 175354, the pit is deepened to a pocket, and the foramen within was large enough to clean out. The foramina on the two sides of the skull proved to communicate across the midline. There is no exit from this passage either dorsally or posteriorly through the orbitosphenoid. In another specimen, USNM 16953, there is only a minute foramen within the depression, and a larger and apparently similar foramen occurs just anterior and medial to the optic foramen. The facts that the passage between the orbits has no other exit and that the position of the foramen is variable suggest that this was part of the venous system and that the aperture is a true interorbital foramen.

The dorsal palatine foramen is hidden. One broken specimen, CM 9809, shows it clearly just inside and ventral to the sphenopalatine foramen. This means that the descending palatine artery and nerve entered the sphenopalatine foramen before passing through the dorsal palatine foramen. The sphenoidal fissure at its opening is separated from the cranial cavity by a wall of bone. The alisphenoid canal enters the sphenoidal fissure laterally. A very slight ridge sets off the dorsal part of the fissure as a separate channel. A small sphenofrontal foramen is present in all undistorted specimens of *Ischyromys*; skulls identified as *Titanotheriomys* are not well enough preserved for me to determine whether the foramen occurs in them also. The sphenofrontal foramen is a short distance posterodorsal to the optic foramen. In some skulls it is entirely within the orbitosphenoid and close to the orbitosphenoid-alisphenoid suture, whereas in others it is in the suture. In all a channel leads gradually downward and forward from it.

The masticatory and buccinator foramina are separate from each other and are at a

substantial distance from the foramen ovale accessorius in specimens of *I. douglassi* from McCarty's Mountain; in CM 1123 the distance is 2.0 mm (see also Black, 1968a: 291, fig. 20 for CM 1122). In one specimen of *Ischyromys* from the middle Oligocene, PU 11383, only a slight bar of bone separates these foramina from the foramen ovale accessorius. In the remaining Orellan specimens of *Ischyromys* and *Titanotheriomys* the masticatory and buccinator foramina are united with the foramen ovale accessorius from which a broad channel runs anterodorsally across the alisphenoid, revealing the course of the masseteric nerve. The foramen ovale accessorius is bounded ventrally by a substantial lateral pterygoid flange, homologous to the lateral ridge in paramyids. The pterygoid fossa is deep in ischyromyids. The foramen ovale is dorsomedial to the foramen ovale accessorius and, in ventral view, is mostly obscured by the lateral pterygoid flange that bridges it. In some specimens there is a small foramen, which probably transmitted a meningeal vessel, medial to the foramen ovale. The entrance to the alisphenoid canal is at the anterior end of the foramen ovale and cannot be seen in ventral view. The middle lacerate foramen, if present, is hidden by the large auditory bulla. An aperture in the middle part of the pterygoid fossa leads to the transverse canal. In most specimens it is directed anteriorly; in one, CM 10966, it heads medially. The transverse canal has other entrances, too, inside the cranium. The largest of these is just behind the basisphenoid-presphenoid suture in the side of the raised cranial floor. A few foramina open into the canal from the surface of the raised portion. These details were seen in one specimen, CM 1123, in which the bone is translucent; upon shining a light through the bone, the matrix-filled canals became apparent.

The posterior opening of the carotid canal is clearly delimited by the basioccipital and the bulla. It is at the anterior end of the same slot that contains the jugular foramen. The bulla has a faint channel running dorsally into the carotid canal. The course of the canal can be seen in one specimen, CM 1123, in which it runs between the basioccipital and the bulla and arches up and over the medially swollen anterior portion of the bulla. It appears to enter the cranial cavity at the level where the medial side of the bulla curves outward. The jugular foramen is directed dorsally at the back of the slot between the basioccipital and the bulla. Black (1968:290, fig. 19) interprets this as the stapedial foramen. However, there must be a jugular foramen to transmit the vagus, accessory, and glossopharyngeal nerves, and the internal jugular vein; this opening is the only possibility. There is no stapedial foramen. The hypoglossal foramen is double except in one specimen of *I. typus,* USNM 15933, in which it is single. The two foramina, of nearly equal size, open into a pit that deepens medially; the anterior foramen faces posterolaterally, the posterior, anterolaterally.

The postglenoid foramen is reduced to a slit-like opening with a major axis measuring 1.5 mm. It is enclosed within the squamosal. A channel can be traced from this foramen through the bone to the single temporal foramen (USNM 175352). In several specimens there seems to be a postalar fissure between the alisphenoid bone and the front of the bulla (AMNH 694 and MCZ 17202 show it clearly). The temporal foramen, single in most specimens, is primarily in the squamosal bone; the squamoso-parietal suture descends into it on the medial side. Its anterior end is above the posterior part of the postglenoid foramen, and its major axis ranges from 2.5 to 3.0 mm. In one specimen, AMNH 694, a second minute foramen is present behind it in the squamosal bone. The squamoso-mastoid foramen is present on the occipital surface; one broken specimen, USNM 175352, has a matrix-filled channel running from it to the temporal foramen; another,

CM 24129, preserves the channel without infilling.

The minute mastoid foramen is in the occipital-mastoid suture well above the level of the top of the foramen magnum. The stylomastoid foramen is well defined and very deep because the bulla is large and the mastoid element inflated.

Discussion of the Ischyromyidae

There is ample skull material of *Ischyromys* to permit thorough description of its morphology. With respect to the cranial foramina, ischyromyids and paramyids are so different from each other that I must agree with those (*e.g.*, Wood, 1965; Wilson, 1949c; Schaub, 1958) who consider them to be separate groups of equivalent rank. I did not find any differences in cranial foramina which would distinguish *Ischyromys* from *Titanotheriomys*.

The ratio of length of the incisive foramina to diastemal length has a range that overlaps that of *Ischyrotomus* and *Manitsha* but does not overlap those of *Paramys, Reithroparamys,* and *Sciuravus*. The lateral margins of the incisive foramina are intersected farther posteriorly by the premaxillary-maxillary suture in ischyromyids. The pair of major posterior palatine foramina are on the maxillary-palatine suture and are usually farther forward relative to the cheek teeth than in paramyids and *Sciuravus*. In ischyromyids the posterior extremity of the maxilla is appressed to the pterygoid extension of the palatine. There is a slit between them which may be homologus to the posterior maxillary notch in paramyids and *Sciuravus*.

In side view the ischyromyid infraorbital foramen is inclined, not vertical as in paramyids and *Sciuravus*. The absolute lengths of the major axes are about the same as in paramyids although the skull size is smaller in ischyromyids; if only the vertical dimension is considered, the length in ischyromyids is shorter than that in paramyids.

Relative to the cheek teeth, the major foramina of the orbit—the optic, ethmoid, and sphenopalatine—are considerably farther forward than in paramyids and *Sciuravus*. The sphenopalatine is bordered by a fused maxilla and palatine and is met posteriorly by the orbitosphenoid; these features differ in paramyids and *Sciuravus*. The dorsal palatine foramen is internal to the sphenopalatine, whereas in paramyids the two foramina are within a single depression, and in *Sciuravus* they are separated. In ischyromyids the posterior palatine foramen, through which the descending palatine artery and nerve emerge, is anterior to its position in paramyids and *Sciuravus*. The depression in the orbitosphenoid in front of the optic foramen for the rectus muscles of the eye and the interorbital foramen accompanying it do not occur in paramyids or *Sciuravus*. The sphenofrontal foramen is small and, in some specimens, entirely within the orbitosphenoid. Where seen in paramyids and *Sciuravus*, it is relatively larger and always in the orbitosphenoid-alisphenoid suture.

Masticatory and buccinator foramina are united with the foramen ovale accessorius in most specimens. When both foramina are present, the channels leading to them through the alisphenoid bone are very short in comparison to those of paramyids but similar to those of *Sciuravus*. The foramen ovale accessorius is present in ischyromyids and in some paramyids, but lacking in *Sciuravus*. In ischyromyids the external pterygoid flange is very well developed and reaches the bulla. The mandibular division of the trigeminal nerve emerged from the foramen ovale, bent laterally, and passed through the foramen ovale accessorius in the extended flange.

The entrance to the transverse canal is separated from the alisphenoid canal. It is possible to picture the transition from a condition like that found in *Ischyrotomus* and *Sciuravus* to this arrangement. As the external pterygoid flange extended and the pterygoid fossa developed for muscle at-

tachment, the entrance to the alisphenoid canal moved as far back as the foramen ovale. The foramen ovale, through which the mandibular division of the trigeminal nerve passes, acted as a barrier to further extension.

The absence of a stapedial foramen indicates that ischyromyids lacked the stapedial artery, and the ophthalmic artery must have arisen, therefore, from the internal carotid. In paramyids and *Sciuravus* a channel for the artery crosses the promontorium. A double hypoglossal foramen occurs in ischyromyids, *Reithroparamys*, and *Ischyrotomus*.

Although the postglenoid foramen is similar in length to those measured in paramyids, it is reduced in width; this suggests that the major course of the venous system that drains the cranial cavity has shifted away from it. There is one large temporal foramen rather than a few small ones as in paramyids. The post-alar fissure and the squamoso-mastoid foramen do not occur in paramyids or *Sciuravus*.

CYLINDRODONTIDAE

Specimens examined:

Ardynomys occidentalis (Fig. 10): Chadron Formation equivalent: CM 1055 npo, 9991 nptc, 9992 c, 16995 npot, 21701 npot.

Cylindrodon fontis: Chadron Formation equivalent: CM 17180 np, 17181 np, 17204 pc. White River Series equivalent: AMNH 14584 pc, 14585 np.

C. sp.: Chadron Formation equivalents: F:AM 79100 s, 79102 np, 79104 np, 79105 np, 79109 s; CM 6546 np, 6643 np, 8904 np.

Pseudocylindrodon medius: Chadron Formation equivalent: CM 1135 np, 10000 np, 10001 s.

P. neglectus: Chadron Formation equivalent: CM 10100 np.

P. sp.: Chadron Formation equivalent: CM 1126 n, 6545 np.

FORAMINA

The ratio of length of the incisive foramina to diastemal length is quite variable in cylindrodontids. Two specimens of *Pseudocylindrodon*, CM 10100 and 6545, have ratios of .37 and .40; the rest range from .50 to .55. The ratio in *Ardynomys* ranges from .28 to .44; in *Cylindrodon*, from .28 to .38. The lateral margins of the foramina are intersected near the back in some specimens, and at the back in others, by the premaxillary-maxillary suture. The suture runs laterally and somewhat posteriorly away from them.

The pair of posterior palatine foramina is in the maxillary-palatine suture medial to the middle part of the first molars. In a few specimens of *Cylindrodon* it is slightly farther posterior, medial to the junction of the first and second molars. The maxilla ends in a point behind the cheek teeth, and in most specimens it is so closely appressed to the pterygoid extension of the palatine that there is neither a posterior maxillary notch nor a foramen. In one specimen of *Pseudocylindrodon*, CM 10001, a posterior maxillary foramen is visible.

In front view the infraorbital foramen is approximately circular with some flattening on the dorsomedial side so that the major axis appears to slant outward. The axis has a wide size range; in *Pseudocylindrodon* from 1.2 to 1.6 mm; in *Ardynomys*, a sample of only two, around 2.0 mm; in *Cylindrodon* from 0.9 to 1.7 mm. In side view the foramen is approximately vertical. In one specimen of *Cylindrodon*, F:AM 79104, the foramen is double on both sides. The anterior alveolar foramen is in the curve made by the orbital wall and floor. It is within the infraorbital foramen and is directed anteromedially in *Pseudocylindrodon* and *Cylindrodon*; in one specimen of *Cylindrodon*, CM 17180, it is almost in front of the infraorbital foramen and heads medially. In *Ardynomys* the foramen is farther posterior and is directed even more medially.
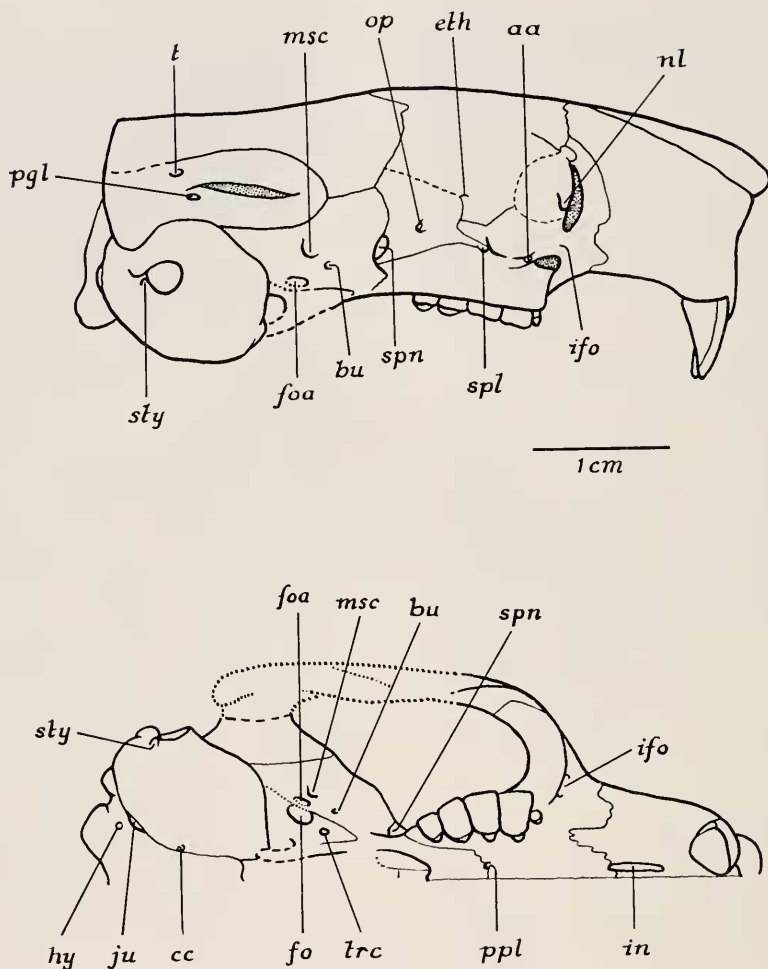
Figure 10. *Ardynomys occidentalis* (composite of all specimens examined; CM 9991 used as base). See Fig. 1 for key to foramina.

The nasolachrymal foramen is dorsal to the infraorbital. The maxilla may participate in its anterior margin, but I cannot determine this for certain. Some specimens have a slight channel leading down into the foramen; others have none. The canal inside the bone runs anteroventrally past the infraorbital foramen; then it plunges medially under the arch of the incisor. For the first part of its course it is external to the incisor alveolus, which reaches back into the orbit in *Ardynomys* and *Cylindrodon*. In the orbital wall of *Pseudocylindrodon*

and in some specimens of *Ardynomys* (Wood, 1970: fig. 4), there is a slight saddle posteroventral to the nasolachrymal foramen; the saddle most likely marks the area of origin of the inferior oblique eye muscle, as in *Marmota*.

The sphenopalatine foramen is dorsal to the posterior part of the first molar in *Pseudocylindrodon* and is directed anteromedially. The maxilla forms its ventral and anterior margins; sutures are not distinct enough for other bones reaching it to be distinguished. The position of the foramen

in *Ardynomys* is somewhat variable. In three specimens, CM 1055, 16995, and 21701, it is above the junction of the first and second molars, while Wood (1970: fig. 4 of CM 12010) shows it as being dorsal to the anterior part of the second molar. It plunges anteroventrally behind the incisor root capsule. The fused maxilla and palatine forms the border on three sides, and a process from the orbitosphenoid reaches the foramen posteriorly. Specimens of *Cylindrodon* are fragmentary and difficult to interpret; the position of the spheno-palatine foramen seems to differ from individual to individual.

The ethmoid foramen is dorsal to the back of the sphenopalatine in *Pseudo-cylindrodon*, CM 10001, and *Cylindrodon*, CM 17180, and above and about equidistant between the sphenopalatine and optic in *Ardynomys*. It is overhung by a lip from the frontal bone. The orbitosphenoid reaches it posteriorly.

The optic foramen measures 0.5 mm in diameter in *Pseudocylindrodon*, CM 10001; it is dorsal to the junction of the second and third molars and very close to the orbitosphenoid-maxillary suture. In *Ardynomys* its diameter ranges from 0.7 to 0.9 mm, and its position is dorsal to an area ranging from the front part of the third molar to a point slightly posterior to that tooth. Wood (1970: fig. 4) shows the alisphenoid as forming the back of the optic foramen; this is not the case in the specimens I have examined. In one specimen of *Cylindrodon* in which the optic foramen is preserved, CM 17180, it is above the back of the second molar and about 0.5 mm in diameter. In this same specimen there is a depression in front of the optic foramen that is more pronounced on the right side than on the left. Presumably this marks the place of origin of the rectus muscles of the eye.

The dorsal palatine foramen is hidden in all three genera. There is evidence in one specimen of *Ardynomys*, CM 1055, that it and the sphenopalatine are contained in a single depression, as in *Paramys*. The sphenoidal fissure at its entrance is open medially into the cranial cavity; the opening extends a short distance in front of the margin of the fissure. This condition probably occurs in *Cylindrodon* also. Burke (1936:139) indicated two openings in this region in *Ardynomys*, CM 1055, not recognizing that the partition between them was a mineral-filled fracture; the specimen has a normal, single sphenoidal fissure.

In *Pseudocylindrodon* the minute spheno-frontal foramen is level with but quite far behind the top of the optic foramen, and it may be on the alisphenoid-orbitosphenoid suture although this is indistinct in all specimens. A channel leads anteroventrally from it. I have found the foramen in one specimen of *Ardynomys*, CM 21701, at the point of intersection of the orbitosphenoid, parietal, and alisphenoid bones; it is very small. The foramen seems to be absent in other specimens of *Ardynomys* and in *Cylindrodon*.

The masticatory and buccinator foramina are separate, and relatively close to the foramen ovale, about 1.0 mm from it. A broad channel runs anterodorsally from the masticatory foramen; a short one proceeds forward from the buccinator. Burke (1936: 139; and 1938:260) identified the buccinator as the masticatory and did not detect the masticatory foramen. The existence of a foramen ovale accessorius is uncertain. The lateral pterygoid ridge is expanded into a flange, and what remains of it defines the anterior end of a foramen or at least a notch. The flange may have reached the bulla, in which case there would have been a foramen.

The transverse canal, as such, has been lost, being reduced to a foramen that opens directly into the cranial cavity from the middle of the moderately deep pterygoid fossa. This is seen clearly in a specimen of *Ardynomys*, CM 21701, in which the inside of the cranium is partially cleaned out. Burke (1936:139; and 1938:259) incorrectly identified this foramen in the pterygoid

fossa as the sphenopterygoid. The alisphenoid canal is small and begins just anteroventral to the foramen ovale. It is clearly defined in *Pseudocylindrodon* and *Cylindrodon*. In *Ardynomys* the wall separating it from the cranial cavity is almost gone; in CM 1055 little more than a strut of bone internal to the buccinator foramen is left. The middle lacerate foramen, if present, is covered by the tympanic bulla. In *Ardynomys* and *Cylindrodon* a foramen of uncertain function pierces the side of the basisphenoid just anterior to the bulla; it is hidden by the hamular process in Figure 10.

The posterior opening of the carotid canal is very small and is separate from the jugular foramen. In *Pseudocylindrodon* the aperture seems to be between the bulla and the basioccipital. In *Ardynomys* and *Cylindrodon* a short channel leads anterodorsally across the medial side of the bulla to the canal. The canal enters and runs anteriorly through the periotic in *Ardynomys;* its course can be seen in one broken specimen, CM 9991. It also enters the periotic in at least one specimen of *Cylindrodon*, CM 17204. There is no stapedial foramen. The hypoglossal foramen is minute in *Pseudocylindrodon* and seems to be situated on the margin of the jugular foramen. The region is somewhat damaged, and this interpretation could be incorrect. In the other two genera it is more medial; in one specimen of *Ardynomys*, CM 9991, it is single on the left side and double on the right; the two foramina face anteriorly into a single depression.

The postglenoid foramen is within the squamosal bone. In *Pseudocylindrodon*, CM 10001, the major axis measures 0.6 mm; in two specimens of *Ardynomys*, 1.1 mm. The temporal foramen is about 1.0 mm long in one specimen of *Pseudocylindrodon* and 0.8 and 1.3 mm in two specimens of *Ardynomys*. In all specimens the region is too crushed for the possible presence of other, smaller temporal foramina to be detected. In *Ardynomys*, at least, the parietal-squamosal suture does not dip down far enough to reach the foramen. Burke (1938:258) stated that in *Pseudocylindrodon* the foramen apparently "marks the suture between the parietal and squamosal." The suture is not visible, however, and his surmise is doubtful. He (1936: 136) calls the foramen a subsquamosal in *Ardynomys*. The squamoso-mastoid foramen is conspicuous in all three genera. In one specimen of *Cylindrodon*, CM 17204, the squamosal is broken away, and the channel from this foramen to the temporal foramen can clearly be seen in the surface of the underlying bone.

The mastoid foramen is probably present but too minute to be found. The stylomastoid foramen is anteroventral to the low mastoid process just behind the external auditory opening.

Discussion of the Cylindrodontidae

The three genera of cylindrodontid rodents examined are very similar to one another in their cranial foramina. They are quite different from paramyids and *Sciuravus* and in some features resemble the ischyromyids.

The ratio of incisive foramen length to diastemal length has a great range. It includes the ranges of *Paramys, Reithroparamys,* and *Sciuravus,* has a slight overlap at the low end with that of ischyromyids, and does not overlap the range of the other paramyids measured. The margins of the foramina are intersected very far back by the premaxillary-maxillary suture, as in ischyromyids. The posterior palatine foramina are on the maxillary-palatine suture, as they are in *Ischyrotomus, Pseudotomus,* and ischyromyids. Relative to the cheek teeth they are situated as in paramyids and are slightly anterior to the position in *Sciuravus.* The posterior maxillary foramen is present in *Pseudocylindrodon*. In *Ardynomys* and *Cylindrodon* the end of the maxilla is appressed to the pterygoid extension of the palatine as in ischyromyids, but there is no aperture between them.

The infraorbital foramen is nearly vertical, as in paramyids and *Sciuravus*. The orbital foramina, as in ischyromyids, are considerably farther forward relative to the cheek teeth than in paramyids and *Sciuravus*. The sphenopalatine foramen is bounded by a fused maxilla and palatine, and is met posteriorly by the orbitosphenoid; both characters occur in ischyromyids and not in paramyids and *Sciuravus*. The sphenofrontal foramen is minute in *Pseudocylindrodon* as in ischyromyids, and it is absent in the other cylindrodontids.

The reduction of bone internal to the sphenoidal fissure and to the alisphenoid bone does not occur either in paramyids or in ischyromyids. The masticatory and buccinator foramina are separate as in paramyids, but they are close to the foramen ovale as are those seen in *Sciuravus* and the earliest skulls of ischyromyids. The development of a pterygoid fossa with a foramen, presumably leading to the transverse canal, in the middle of it, the possible presence of a foramen ovale accessorius, and the position and relative size of the entrance to the alisphenoid canal are as in ischyromyids. The foramen in the basisphenoid just anterior to the front of the bulla may be homologous to the medial division of the middle lacerate foramen in paramyids.

The separation of the entrance to the carotid canal from that to the jugular foramen, and the passage of the canal through the periotic, which occur in *Ardynomys* and *Cylindrodon,* are different from the conditions in paramyids, *Sciuravus,* and ischyromyids. Both cylindrodontids and ischyromyids lack the stapedial foramen. The hypoglossal foramen is usually single, as in *Sciuravus* and some paramyids, whereas in ischyromyids the foramen is always double.

The shift in emphasis of the venous system away from the postglenoid foramen, the presence of a single temporal foramen below the parietal-squamosal suture, and the opening-up of a squamoso-mastoid foramen are all changes from the paramyid condition that occur in ischyromyids.

PROSCIURIDAE

Specimens examined:
> *Prosciurus relictus*: Cedar Creek Member, White River Formation: KU 8333 npo, 8345 npo.
> *P.* aff. *saskatchewaensis* (Fig. 11b): Orella Member, Brule Formation: AMNH 1429 c.
> *P.* cf. *vetustus*: Orella Member, Brule Formation: FMNH, PM 14674 np.
> *P.* sp. (Fig. 11a): Orella Member, Brule Formation: SDSM 62365 npo.
> ?*Cedromus* sp.: Cedar Creek Member, White River Formation: KU 8342 ptc.

FORAMINA

The ratio of length of the incisive foramina to diastemal length ranges from .39 to .48. The lateral margins of the foramina are intersected near the back by the premaxillary-maxillary suture, which runs laterally and somewhat posteriorly away from them.

The pair of major posterior palatine foramina is in the palatine medial to an area ranging from the posterior portions of the second molars to the anterior portions of the third molars. A second, smaller pair is medial to the third molars. The maxilla ends in a blunt point, and a posterior maxillary notch is formed between it and the pterygoid extension of the palatine.

In front view, the infraorbital foramen is nearly circular. The major axis measures 1.3 mm, and it is inclined so that the top of the foramen is farther lateral than the bottom. In side view the foramen slopes forward slightly. The anterior alveolar foramen, which is in the curve made by the orbital floor and wall, lies either within or a short distance behind the infraorbital foramen and is directed anteromedially.

The nasolachrymal foramen is dorsal to the infraorbital. A channel descends the face of the lachrymal bone into the fora-
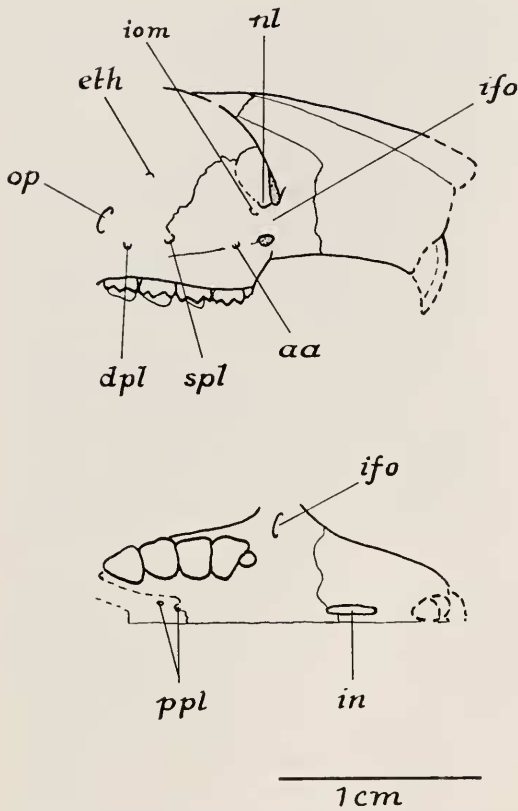
Figure 11a. *Prosciurus* sp. (SDSM 62365). See Fig. 1 for key to foramina.

Figure 11b. *Prosciurus* aff. *saskatchewaensis* (AMNH 1429; modified from Wood, 1937: plate 13; lateral view additional). See Fig. 1 for key to foramina.

men. Immediately posterior and slightly ventral to the nasolachrymal foramen is a depression in the bone, whether in the maxilla or lachrymal cannot be determined. This was apparently the area of origin of the inferior oblique eye muscle.

The sphenopalatine foramen is above the middle or the posterior part of the second molar. The maxillary-frontal suture intersects it dorsally; the orbital portion of the palatine reaches it posteriorly, and the orbitosphenoid is wholly excluded from its margin. The ethmoid foramen is dorsal to the posterior part of the second molar. It is within the frontal bone and overhung by a lip of that bone. The orbitosphenoid does not reach it posteriorly. Only the anterior part of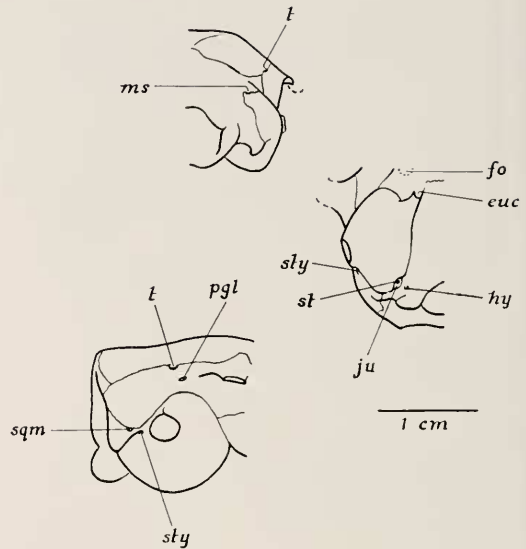 the optic foramen is preserved in one specimen, SDSM 62365; it is dorsal to the posterior part of the third molar. Although damaged, the foramen was about 1.5 mm long. In two specimens, KU 8333 and 8345, a depression is present immediately anterior to the optic foramen. It contains a minute interorbital foramen and was probably the area of origin for the rectus muscles of the eye.

The dorsal palatine foramen in the orbital floor is above the posterior part of the third molar and lies within the palatine near the maxillary suture in KU 8342, and in the suture in KU 8333. The sphenoidal fissure is dorsal and wholly posterior to the last molar. The region in which the sphenofrontal foramen would be situated is not preserved in any of the specimens.

My interpretation of the orbital region is at variance with Galbreath's identification of certain foramina in *Prosciurus relictus*, KU 8333 (Galbreath, 1953:53, fig. 16). The foramen he labeled the optic is the interorbital, and the sphenoidal fissure is the optic foramen. The posterior of two foramina shown in the orbital floor is the

dorsal palatine; the maxillary-palatine suture is not very clear in the specimen, but it seems to pass through this foramen. The anterior aperture is an exposed root of the second molar.

The alisphenoid region is preserved only in KU 8342. Galbreath (1953:60, fig. 19) identified the most conspicuous foramen as the masticatory. It is situated rather far ventrally in comparison with the masticatory in other rodent skulls examined, and it faces anteriorly; both the position and orientation would indicate that it is the buccinator foramen. However, a second aperture leading from the alisphenoid canal is present anterior to it near the edge of the alisphenoid; this opening is either the buccinator foramen or a foramen that does not occur in any of the other rodent skulls I have examined. The problem of identifying these foramina with certainty cannot be solved because the region in which the mastoid foramen would normally occur is damaged. The area labeled by Galbreath as the buccinator foramen is a damaged foramen ovale accessorius.

The shallow pterygoid fossa is partially preserved in this same specimen. The foramen ovale is situated posterolaterally within the fossa. The alisphenoid canal begins ventral to the anterior end of the foramen ovale, the transverse canal medial to it. The middle lacerate foramen is absent or covered by the tympanic bulla.

The carotid canal, if present, shares an opening with the jugular foramen and is very narrow. The jugular foramen appears to be broader than in other protrogomorphs, but this is due to the presence of the stapedial foramen lateral and slightly dorsal to it in a common depression. The hypoglossal foramen is single and medial to the jugular.

The postglenoid foramen, which is hardly more than a slit in the squamosal, is in line with the zygomatic root; its major axis measures 0.8 mm. There is one temporal foramen in the squamoso-parietal suture dorsal and slightly posterior to the postglenoid foramen. The squamosal is broken off on the left side of the specimen, and a conspicuous channel connecting the two foramina can be seen on the surface of the underlying bone. A channel also runs posteroventrally from the postglenoid foramen to the region where the rounded tip of the squamosal meets the mastoid element. This indicates the presence of a squamoso-mastoid foramen.

The mastoid foramen is very dorsally situated in the mastoid-occipital suture. The stylomastoid foramen is in its usual position between the external auditory meatus and the mastoid.

Discussion of the Prosciuridae

The ratio of length of the incisive foramen to diastemal length has a range that includes those of *Paramys*, *Reithroparamys*, and *Sciuravus*. It overlaps the upper end of the ranges in cylindrodontids and it is above those in other protrogomorphs. The major pair of posterior palatine foramina is situated farther posterior relative to the cheek teeth than that of any other protrogomorphous form. The posterior maxillary notch is as in paramyids.

The infraorbital foramen is not vertical as in paramyids and *Sciuravus*. It slopes anteriorly though not as much as that in ischyromyids. The depression for attachment of the inferior oblique eye muscle does not occur in other protrogomorphous rodents, although the site is indicated in *Ischyromys*, *Pseudocylindrodon*, and *Ardynomys*. The sphenopalatine foramen is surrounded by the frontal, maxillary, and palatine bones, as in paramyids and *Sciuravus*, in which the frontal is barely excluded from the dorsal margin; the orbitosphenoid does not reach the foramen in any of these forms. The ethmoid foramen is within the frontal, as in *Sciuravus* and some specimens of *Paramys*. The size of the optic foramen is relatively large for a protrogomorphous rodent. The depression for attachment of the rectus muscles of the eye and the interorbital fora-

men within it are also present in ischyromy-
ids, but not in other protrogomorphs. The
dorsal palatine foramen is separate from
and posterior to the sphenopalatine, as in
Sciuravus.

The pterygoid fossa is shallow and the
foramina within it are situated as in
Ischyrotomus and *Sciuravus.* The stapedial
foramen indicates the presence of a sta-
pedial artery, which was also present in
paramyids and *Sciuravus;* ischyromyids and
cylindrodontids lacked it.

The postglenoid foramen is greatly re-
duced, but a temporal foramen and the
squamoso-mastoid foramen are present.
This arrangement is unlike that of para-
myids and sciuravids and similar to that
of ischyromyids and cylindrodontids.

APLODONTOIDEA

Specimens examined:
   Aplodontidae:
   Allomys nitens (Fig. 12): John Day
      Formation: UCMP 1100 np.
   Liodontia furlongi: Barstovian deposits,
      Nevada: UCMP 61716 s, 75666 np.
   Aplodontia rufa: Recent: UNSM, Z.M.
      275: MCZ 799, 1893, 5645, 6369, 6822,
      13183, 17810, 18352.
   Mylagaulidae:
      The taxonomy of mylagaulids is at
   present so uncertain that I prefer to list
   the specimens examined in stratigraphic
   order.
   Rosebud Formation:
   Promylagaulus riggsi (see McGrew,
      1941:6 for figure): FMNH, P 26256
      npo.
   Marsland Formation and equivalents:
   Mesogaulus laevis: UNSM 04953 npot,
      04954 p; F:AM 65004 npo.
   Sheep Creek Formation:
   Promylagaulus novellus[1]: F:AM 65001
      np.
   Mesogaulus sp.: F:AM 65002 potc,

[1] This species has heretofore been placed in the
genus *Mylagaulus*, but Stout (personal communi-
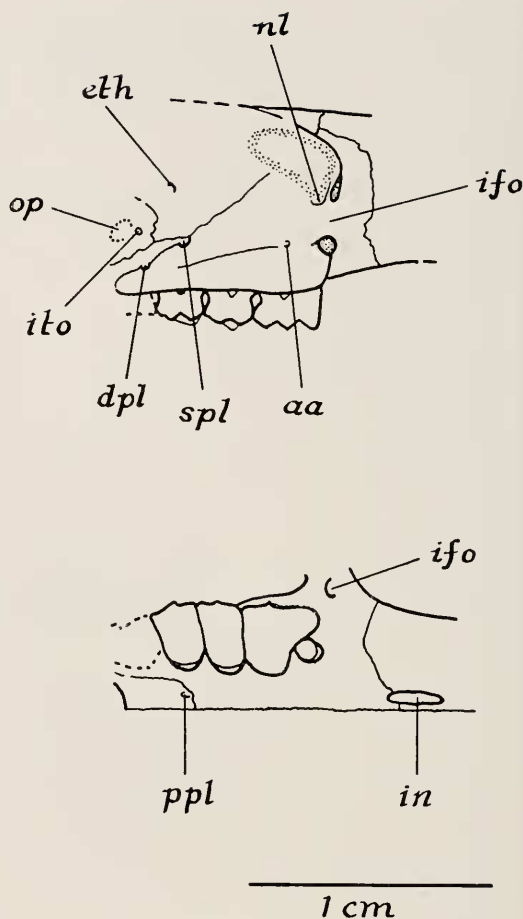cation) now places it in the genus *Promylagaulus.*

Figure 12. *Allomys nitens* (UCMP 1100). See Fig. 1 for
key to foramina.

65003 s, 65005 np, 65006 s, 65007 np,
   65011 nptc.
Mylagaulus vetus: AMNH 18903 pot,
   18904 np, 20507 npt.
Mylagaulus laevis (Fig. 13): AMNH
   17576 s.
Ceratogaulus rhinocerus: AMNH 18899
   p.
large mylagaulid: F:AM 65016 s, 65017
   nptc.
Pawnee Creek Formation:
Ceratogaulus rhinocerus: AMNH 9456
   (type) npt.
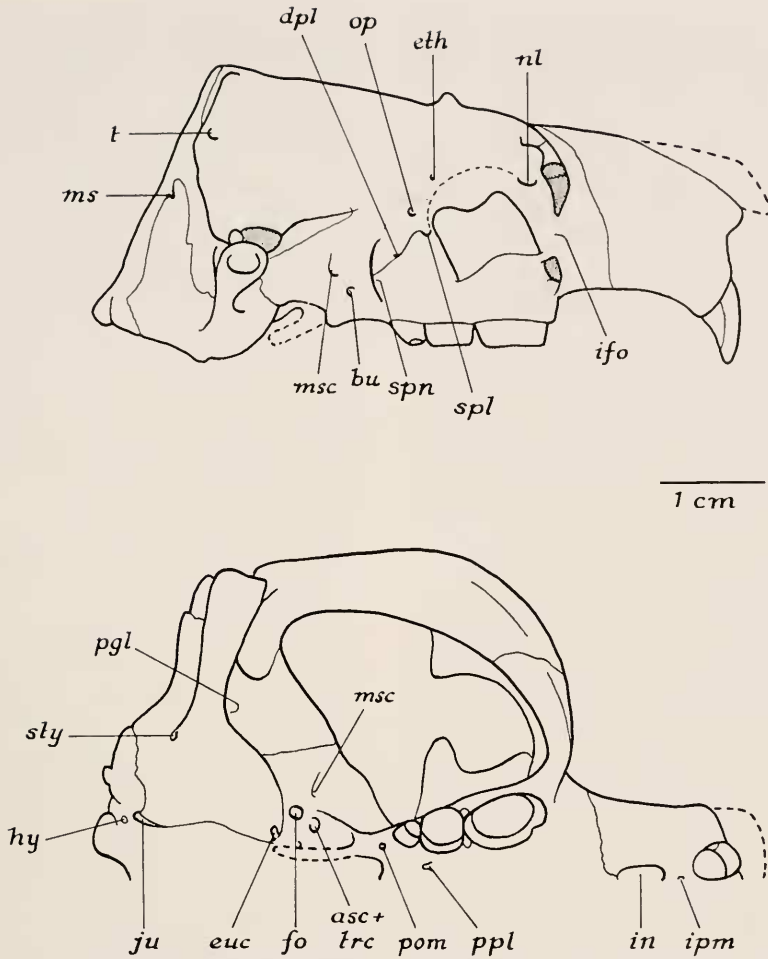*Mylagaulus laevis*: AMNH 9043 (type)
   np.

Figure 13. *Mylagaulus laevis* (mostly based on AMNH 17576; basicranium restored from various specimens). See Fig. 1 for key to foramina.

Barstovian deposits, Montana:
  Mylagaulus douglassi: UCMP 44694 npo.
  Mylagaulus sp.: PU 18186 s.
Deep River beds:
  Mylagaulus sp.: AMNH 21307 s.
Valentine Formation:
  Mylagaulus sp.: UNSM 04957 n.
Burge Member, Valentine Formation:
  Mylagaulus sp.: UNSM 04956 np; F:AM 65009 potc, 65010 potc, 65012 s, 65013 tc.
Clarendonian deposits, South Dakota:
  Mylagaulus sp.: UCMP 32323 potc.

Ash Hollow Formation:
  Mylagaulus sp.: UNSM 04955 n.
Kimball Formation:
  Mylagaulus sp.: UNSM 04958 npo.
Pliocene deposits, Nebraska:
  Mylagaulus sp.: F:AM 65008 np., 65014 npo, 65015 np.

FORAMINA

The interpremaxillary foramen is a conspicuous feature in *Aplodontia*. It is quite variable in the fossils. *Liodontia* seems to have a small one; the region is not pre-

served in *Allomys*. In mylagaulids a pit and sometimes a minute foramen are present in its position. *Promylagaulus* lacks the foramen.

The ratio of length of the incisive foramina to diastemal length in aplodontoids ranges from .28 to .43, and values are quite evenly distributed. The ratio does not vary with the geologic age of the specimens. No ratio can be obtained for *Allomys*; *Promylagaulus* falls at .33. In *Allomys*, as in all aplodontids, the lateral margins of the foramina are intersected at the back by the premaxillary-maxillary suture, which runs laterally and somewhat posteriorly away from them. In most mylagaulids the ends of the foramina are intersected by the suture, which runs posteriorly from them; in some specimens the maxilla does not appear to reach the foramina, which may be entirely within the premaxillary bones.

The major pair of posterior palatine foramina is medial to an area ranging from the middle of the second molars to the anterior part of the third molars in all aplodontoids. In *Allomys* and in juvenile specimens of *Aplodontia* the pair is very close to the maxillary-palatine suture, but within the palatine; the suture is not visible in adult aplodontoids. In one specimen of *Liodontia* a second, smaller pair is in line with the first pair and medial to the back of the second molars. *Aplodontia* commonly has one or two pairs of small foramina in line with and posterior to the major pair. The maxilla ends behind the cheek teeth in a point, which is fused to the lateral side of the pterygoid region in all but juvenile specimens. The posterior maxillary foramen, enclosed between the two parts, opens above in the floor of the sphenoidal fissure and may have transmitted a palatine vein. The region is not preserved in *Allomys* and is unclear in *Promylagaulus*.

In front view, the infraorbital foramen is of variable shape; it may be elliptical with the major axis running diagonally or horizontally, or it may be nearly round. In *Allomys* the major axis measures 1.8 mm;

in other aplodontids, from 2.5 to 4.0 mm, the low values being from juveniles; in *Promylagaulus*, 1.2 mm; and in other mylagaulids, from 1.9 to 4.8 mm. In side view the foramen is nearly vertical. The anterior alveolar foramen in *Allomys* is above the fourth premolar in the curve formed by the orbital wall and floor. The position of the foramen is extremely variable in *Aplodontia*; it is seen most commonly in the medial wall of the infraorbital foramen. The foramen was not seen in most mylagaulid specimens; it is probably obscured by the great alveolus of the fourth premolar. In one specimen, UCMP 32323, it lies in the medial wall of the infraorbital foramen.

The lachrymal region is very well preserved in most specimens. In *Allomys* the lower margin of the nasolachrymal foramen is medial to the upper part of the infraorbital. Sutures in the area are unclear, and it is not possible to determine which bones surround the foramen. In *Promylagaulus* the nasolachrymal is considerably farther dorsal. In other aplodontids and mylagaulids it is a short distance above and slightly posterior to the infraorbital, and a channel leads ventromedially down the face of the bone to it. In one juvenile specimen of *Aplodontia*, MCZ 5645, sutures can be seen; the maxilla forms the anteroventral edge of the foramen. In one mylagaulid, PU 18186, the first part of the canal is exposed. It slopes to a point just anteroventral to the infraorbital foramen where it turns anteromedially. In many large specimens of *Aplodontia* a rounded notch is present in the posterior projection of the lachrymal; clearly it transmitted a vessel or nerve to the top of the head.

In order to render the positions of the orbital foramina intelligible it is necessary to digress and to explain the mode of cheek tooth replacement in mylagaulids. The cheek teeth of mylagaulids are very hypsodont, but the fourth premolar greatly surpasses the molars in this respect. This tooth is shaped like a long wedge, and, as

it erupts, the first molar and then possibly the second are eliminated by interdental wear. A cheek tooth dentition may contain P^4, M^1, M^2, M^3, or P^4, M^2, M^3, or just P^4, M^3. The apparent differences in position of the orbital foramina relative to the cheek teeth are determined by the degree of encroachment of the fourth premolar on the molars. In contrast, the cheek teeth of *Liodontia* and *Aplodontia* are all hypselodont; the orbital foramina are high and above the alveoli, and major differences in position do not occur.

The sphenopalatine foramen is above the second molar in *Allomys;* the orbital process of the palatine reaches it posteriorly, and the orbitosphenoid is excluded from its margin. In *Aplodontia* the foramen is dorsal to the posterior part of the premolar; the cheek tooth alveoli obscure all sutures in the region. In *Promylagaulus* the foramen is dorsal to the junction of the first and second molars, whereas in other mylagaulids the foramen is above the second molar, posterior to the great alveolus of the last premolar. In UCMP 32323, in which the premolar is almost fully erupted and the second molar worn away, the foramen is above the posterior part of the premolar. Orbital sutures are fused in all specimens.

The ethmoid foramen is dorsal to the posterior part of the second molar in *Allomys;* sutures in its vicinity cannot be determined. The foramen is overhung by a slight lip of bone. In *Aplodontia* the foramen is posterodorsal to the spheno-palatine and above the junction of the first and second molars. There are commonly two or three minute foramina close together; the number may differ on the two sides of a skull, and the orientation of individual apertures in such a group may differ substantially. In juvenile specimens the ethmoid foramen is within the frontal bone. I could not identify the ethmoid foramen in *Promylagaulus*. In other mylagaulids it is dorsal and slightly anterior to the sphenopalatine foramen; it opens upward. Only the anteroventral margin of the optic foramen is preserved in *Allomys* and *Promylagaulus;* it is dorsal to the posterior part of the third molar. The curvature of both margins suggests that the optic foramina were about 1.0 mm in diameter. In *Aplodontia* the optic foramen is dorsal to an area ranging from the middle of the second molar to the front part of the third molar, and it is nearly reached by the alveolus of the second molar. The diameter of the foramen ranges from 1.0 to 1.5 mm. Juvenile specimens demonstrate that it is wholly within the orbitosphenoid. In mylagaulids, other than *Promylagaulus*, the optic foramen is close behind the spheno-palatine and dorsal to the same area as in *Aplodontia;* it ranges in size from 0.6 to 0.9 mm.

An interorbital foramen is present in *Allomys* immediately in front of the optic. McGrew (1941:7, fig. 2) identifies it as the optic foramen, but it has no connection with the cranial cavity; I believe that his sphenoidal fissure is the optic foramen and that the sphenoidal fissure itself is missing from the specimen he examined. In mature specimens of *Aplodontia* a short process of bone and a pit anterior to it are present in front of the optic foramen; this is probably the site of origin of the rectus muscles of the eye.

The dorsal palatine foramen is on the palatine-maxillary suture dorsal to the anterior part of the third molar in *Allomys*. It is hidden in *Aplodontia* but can be located by pushing a hair through the posterior palatine foramen. The hair comes out above the third molar in the crevice between the molar alveolus and the orbitosphenoid. The foramen cannot be seen in most mylagaulids; when visible, it is dorsal to the third molar. The specimens of *Allomys* and *Promylagaulus* are broken off at this point. The sphenoidal fissure at its entrance is open medially into the cranial cavity in mylagaulids and *Aplodontia*. There is no sphenofrontal foramen.

The masticatory foramen is separated from the buccinator by a distance of over

2.0 mm in some specimens of mylagaulids and of *Aplodontia*. The buccinator foramen is much smaller than the masticatory in the latter. Although the pterygoid fossa is deep, the lateral flange is short, and a foramen ovale accessorius is lacking.

In mylagaulids and *Aplodontia* the alisphenoid canal is very large and situated anterolaterally in the fossa. The aperture of the transverse canal is just inside the medial border of the alisphenoid canal. In mylagaulids the canal is very broad; one broken specimen, PU 18186, reveals a pair of channels running posterodorsally from the canal into the cranium. This same specimen demonstrates that, as in *Aplodontia*, the masseteric and buccinator portion of the mandibular nerve splits off before that nerve emerges from the foramen ovale. The foramen ovale is situated posterolaterally in the pterygoid fossa. There is a slight gap between the roof of the fossa and the bulla. In one mylagaulid specimen, UCMP 32323, the foramen ovale is confluent with this gap, and in *Aplodontia* the foramen may be separate, or confluent, on one or both sides of the skull.

Aplodontia lacks both carotid and stapedial arteries (Guthrie, 1969; Bugge, 1971b); however, in many specimens a minute foramen can be seen in the medial wall of the periotic at the anterior end of the jugular foramen. This foramen was noted in one mylagaulid specimen, AMNH 17576; in some others a separate, minute opening is present between the bulla and the basioccipital. It is possible that these foramina are remnants of embryonic arterial passageways. The hypoglossal foramen is usually double, but occasionally single.

The postglenoid foramen is between the squamosal and the tympanic. Although it resembles a post-alar fissure, it is too far dorsal to be that aperture. Temporal foramina are present near the occipital crest. A single foramen is the most common condition, but two foramina either in an anteroposterior line or side by side are not unusual. In one specimen of *Aplodontia*, MCZ 5645, a channel connecting the temporal and postglenoid foramina can be seen inside the cranium.

The mastoid foramen is in the occipital-mastoid suture slightly above the level of the top of the foramen magnum. The stylomastoid foramen is in its usual position, although the external auditory meatus is greatly extended beyond it.

Discussion of the Aplodontoidea

A conspicuous interpremaxillary foramen, or a distinct depression in this position, which is present in many aplodontoids does not occur in other protrogomorphous rodents. The ratio of length of the incisive foramina to diastemal length has a range that nearly matches those of *Ardynomys* and *Cylindrodon*. It is below the ranges in *Paramys*, *Reithroparamys*, *Sciuravus*, *Pseudocylindrodon*, and prosciurids, and above that in *Ischyrotomus*; it overlaps the high end of the range in ischyromyids. The posterior palatine foramina are farther posterior than in other protrogomorphs except prosciurids. The posterior maxillary foramen is similar only to that of *Pseudocylindrodon* within this group.

The infraorbital foramen is vertical, and of a size range similar to that in most protrogomorphs. The ethmoid foramen may be entirely within the frontal throughout the aplodontoids, although its position relative to the orbitosphenoid suture can be determined only in juvenile specimens of *Aplodontia*. The foramen is also within the frontal in prosciurids, *Sciuravus*, and some individuals of *Paramys*. The sphenopalatine and optic foramina are considerably farther forward relative to the cheek teeth than in paramyids, but are in positions similar to those in *Sciuravus*, *Ardynomys*, and prosciurids. The size of the optic foramen is approximately as in other protrogomorphs. The interorbital foramen resembles that of ischyromyids and prosciurids. Complete separation of the dorsal palatine

foramen from the sphenopalatine is a resemblance to *Sciuravus* and prosciurids. The sphenofrontal foramen is absent, as in *Ardynomys* and *Cylindrodon* among protrogomorphs. Reduction of bone internal to the sphenoidal fissure is a feature that is also encountered within the suborder. The presence of separate masticatory and buccinator foramina and the absence of the foramen ovale accessorius are characters shared with paramyids and *Sciuravus*.

The arrangement of foramina in the pterygoid fossa is very similar to that occurring in *Ischyrotomus*, *Sciuravus*, and prosciurids. It is very different from that of ischyromyids and cylindrodontids. The positions of the postglenoid foramen and the temporal foramina differ from those seen in other protrogomorphous rodents.

CONCLUSIONS

Cranial foramina vary within definite limits. Those that transmit nerves are always present although their number may increase if a nerve divides inside rather than outside the bone, or decrease if two foramina fuse. Foramina transmitting arteries vary by fusion and by loss when an artery is eliminated; once a new pattern of arterial circulation is fixed, it is perpetuated in the lineage concerned. Foramina transmitting veins are the most plastic in number and presence or absence, within certain bounds imposed by the requirements of circulation. With these principles in mind the characters of the cranial foramina may be used to test ideas on rodent phylogeny and taxonomy. To this end, I present, first, those features that set families and superfamilies apart, one from another, and those that indicate relationships between groups. Next, I briefly discuss each family and superfamily in an endeavor to integrate these data with those presented by various workers on the basis of other structures. Following this, I propose a classification of the groups studied that seems plausible in light of the available evidence.

The Paramyidae, first appearing in the late Paleocene, are the earliest known rodents. Sciuravids, though recovered first from slightly younger strata, are so similar, that I shall consider the families together. The paramyid skulls I have examined represent three of the four subfamilies designated by Wood (1962:11)[1]. They date from the middle early Eocene (Lysite), and later, and therefore may differ in some features from the earliest members of the family. The skulls of *Sciuravus* are of early middle Eocene (Bridger) age and may differ likewise from older members of the Sciuravidae.

The dorsal palatine foramen and sphenopalatine open into a common depression in the three paramyid genera in which the region remains intact. I believe this arrangement to be primitive within the Rodentia. In *Sciuravus* and in all rodent families derived from paramyids (except ischyromyids and cylindrodontids), the dorsal palatine foramen is in the floor of the orbit posterior to the sphenopalatine foramen.

Three patterns of foramina in the pterygoid region occur in paramyids. The inclusion of the foramina within a small depression in *Paramys copei* could well be structurally ancestral to the condition seen in *Ischyrotomus* and *Pseudotomus* and in *Paramys delicatus*. The pterygoid region of *Sciuravus* is like that in *Ischyrotomus* and *Pseudotomus;* from this arrangement of foramina can be derived those in all later rodents.

In *Paramys, Leptotomus, Ischyrotomus,* and *Pseudotomus* a canal is present that begins at the anterior end of the jugular foramen and runs between the basioccipital and periotic. I have called it the carotid canal, since it is so termed in living rodents. However, the mere presence of this canal is no sure evidence that there was

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[1] Wood's fifth subfamily, the Prosciurinae, I exclude from the Paramyidae for reasons given below.

a medial branch of the internal carotid artery running through it; the canal also transmits the inferior petrosal sinus and would be present if either or both of these vessels existed. The fact that some later rodents of apparent paramyid descent have an internal carotid artery in the canal, *e.g.*, ischyromids (almost certainly) and castorids, is evidence that some or all members of the family had the artery.

The auditory region is preserved in the genera above, except *Pseudotomus*. A channel marking the course of the stapedial artery runs across the promontorium from the region of the jugular foramen to the fenestra vestibuli. If the medial branch of the internal carotid artery ran through the carotid canal, then the stapedial branch diverged from it outside, *i.e.*, medial to, the middle ear, as it does in later rodent groups.

Leptotomus has not only a carotid canal and stapedial artery channel, but also a groove marking the course of the promontorial artery. Did this genus have a three-branched internal carotid as has been attributed to early mammals (*cf.*, *e.g.*, Szalay, 1972:71) and to primitive insectivores (McKenna, 1966)? If this is the case, then rodents had a very early origin within the Mammalia or they are derived from an insectivore retaining the medial branch of the internal carotid; the promontorial artery in *Leptotomus* is, then, a primitive relict. Perhaps the genus did not have a third, medial branch of the internal carotid, and the carotid canal transmitted only the inferior petrosal sinus. If this is the case, then the carotid circulation was like that in *Sciuravus*, in which stapedial and promontorial branches are present, but a carotid canal is lacking. This arrangement is like those in living and most fossil insectivores (Tandler, 1899:749; van Kampen, 1905: 422ff.; McDowell, 1958:205), and it is described as primitive for primates (Gregory, 1920; Hill, 1953, 1955; McKenna, 1966:7). If division of the internal carotid within the middle ear is primitive for rodents, too, and

if the third, medial branch was lost prior to their origin, then rodents may be related in some way to these orders. The artery in the carotid canal in paramyids and later rodents is, then, the branch that crosses the promontorium in *Leptotomus* and *Sciuravus*. Examination of the canal transmitting the carotid artery in the array of living rodents reveals a variety of structural detail (Hill, 1935; Wahlert, 1972) which suggests that the carotid canal arose separately in different groups. This is to be expected if the artery did not run in a canal in the earliest rodents.

The ischyromyids and cylindrodontids retain the close association of sphenopalatine and dorsal palatine foramina encountered in paramyids. In both families the orbital foramina are farther anterior relative to the cheek teeth than they are in any other protrogomorphous group. The orbitosphenoid reaches the sphenopalatine in these and in no other groups. The sphenofrontal foramen is reduced or absent; the arrangement of foramina in the pterygoid region is unique to these two families. The association of palatine and sphenopalatine foramina is a primitive feature also encountered in *Paramys*. The presence of a carotid canal in ischyromyids is evidence supporting derivation from the paramyids. The canal is reduced in cylindrodontids, and has a peculiar course in two of the genera.

The prosciurids and aplodontoids form a natural assemblage as regards their foramina, and they have two peculiar features in common. The ethmoid foramen is well within the frontal bone rather than in or near the orbitosphenoid-frontal suture, and the posterior palatine foramina are, in general, farther posterior than in other rodents.

None of the early aplodontids are known from skulls. The fragment of *Allomys* has an interorbital foramen anteroventral to the optic foramen, as do some of the specimens of *Prosciurus*. The fragment of *Promylagaulus* indicates only that the genus is a

side branch of the Mylagaulidae. The arrangement of foramina in mylagaulids is so much like that of *Aplodontia* that, on this basis, the two groups could be placed in one family.

The cranial foramina of prosciurids do not provide any clear evidence as to whether their ancestors were sciuravids or paramyids. Separation of dorsal palatine and sphenopalatine foramina occurs in *Sciuravus*, but this condition in prosciurids could be derived easily from that in paramyids. The position of the ethmoid foramen just within the frontal seems to occur in some paramyids and in *Sciuravus*. The positions of the orbital foramina, relative to the cheek teeth, are different from those of either group. Differences in the pterygoid region indicate that Wood's (1962: 243) suggested derivation of prosciurids from *Paramys delicatus* is unlikely, but this by no means excludes the possibility of descent from some other paramyid.

This is the evidence, based on cranial foramina, that suggests the unity of certain assemblages and their affinities to others. What bearing does it have on the various hypotheses concerning the relationships of the groups discussed that have been proposed on other grounds?[1]

Sciuravids date from the early Eocene Lysite Member of the Wind River Formation. At that time sciuravids and paramyids were so closely related that "... a contemporary taxonomist would never have considered them distinct families" (Wood, 1965:133). The cranial foramina in the two groups are nearly alike even at the beginning of the middle Eocene, when the two are easily separated on the basis of the dentition. The distinctive characteristics of paramyids and *Sciuravus* may well stem from differential retention of primitive

features in these genera and may not be consistent throughout their respective families. Wood believed the Sciuravidae arose from, or near to, the Microparamyinae, a group for which no skulls are known. There is no available evidence that would cast doubt on this conclusion.

Leptotomus with its primitive carotid circulation occupies a special place within the Paramyidae; this is in keeping with Woods' phylogeny (1962:243), which shows it as part of a distinct lineage since early in the family's history. Whether or not the genus should be retained in the Paramyinae cannot be decided without a better sample of paramyid skulls. The primitiveness of the genus makes it an unlikely candidate for the ancestor of *Ischyromys* as proposed by Wood (1962:248).

Ancestry of the ischyromyids has long been in doubt because of dental resemblances to both paramyids and sciuravids. Wood (1962:248) has, after earlier hesitation, advocated a paramyid ancestry. Black (1968a) compared early Oligocene species of *Ischyromys* with paramyids and sciuravids and found so great a similarity to the former that he included the genera of both groups in a single family, the Ischyromyidae. The evidence from cranial foramina, although not conclusive, supports a paramyid ancestry for the family, but striking differences in the arrangement of foramina from that in the known paramyids indicate that the two groups are distinct at the familial level.

The cylindrodontids have been derived from sciuravids by Wood (1955 and 1959). The unique features of the cranial foramina common to cylindrodontids and ischyromyids suggest that the two groups had a common ancestry, which, on the evidence of *Ischyromys*, I suspect to have lain within the Paramyidae.

Wilson (1949b) and Wood (1962) believed that the Prosciuridae (Prosciurinae in their usage) were derived from paramyids. The cranial foramina, as stated above, neither oppose nor support this

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[1] Wilson (1949c) presents an excellent review tracing the history of opinion regarding relationships of all of the groups discussed here. I have not thought it necessary, therefore, to repeat such information, but limit myself to contributions subsequent to his paper.

view; they do suggest, however, that the group is entitled to familial rank, and this is supported by other features. All the following characters differ from those of paramyids: stapedial foramen situated dorsolaterally within jugular foramen; dorsal palatine foramen above third molar; optic foramen, in part, dorsal to third molar; lateral pterygoid ridge prominent, possibly enclosing foramen ovale accessorius (in *Reithroparamys* and *Leptotomus* among paramyids); ethmoid foramen situated well within frontal; cranium distinctly domed in profile; flattened lyrate area on skull roof; postorbital process present and strong; auditory bullae inflated; incisor enamel uniserial; masseteric fossa extending ventral to first molar (only in *Manitsha* among paramyids). I agree, therefore, with Wilson (1949c) and with Schaub (1958) that familial rank is warranted.

The Aplodontidae appear in the latest Eocene. Resemblances to the prosciurids were demonstrated in detail by Wilson (1949a and c). Wood (1962:243, 247) suggested derivation of the group from a prosciurine, probably *Mytonomys*, in the middle late Eocene. Although Black (1968b), on the basis of new material, demonstrated that *Mytonomys* is not a prosciurid, the cranial foramina provide strong support for the descent of aplodontids from prosciurids. Mylagaulids and aplodontids are so similar that I am in complete agreement with those who derive the former from aplodontids in the late Oligocene. The three groups are very closely related, and can be considered as members of a single superfamily.

There remains for consideration the bearing on formal taxonomy of the evidence reviewed. Certain changes within the suborder Protrogomorpha would seem to be required, and the following arrangement of the groups studied emerges:

Protrogomorpha
  Ischyromyoidea
    Paramyidae

    Ischyromyidae
      Ischyromyinae
      Cylindrodontinae
    Sciuravidae
    Protoptychidae (*inc. sed.*)
  Aplodontoidea
    Prosciuridae
    Aplodontidae
      Aplodontinae
      Mylagaulinae

Subdivision of the Protrogomorpha into two superfamilies separates the ancestral and primitive, derived families from the relatively more advanced aplodontoids. Until more forms of protoptychids are known, I prefer to retain the family within the Protrogomorpha (Wahlert, 1973) and have placed it tentatively in the superfamily Ischyromyoidea. In view of the similarities between ischyromyids and cylindrodontids, I propose that the rank of each group be reduced to subfamily and that they be combined under the older family name, Ischyromyidae Alston, 1876. This association, based on the foramina, merits further study from other evidence.

The cranial foramina of aplodontids and mylagaulids are so alike that I have likewise reduced the rank of each group to subfamily and united them under the older family name, Aplodontidae Trouessart, 1897 (= Haploodontini Brandt, 1855). The prosciurids have been included in a superfamily with them to express the many characters unique to the two families.

The cranial foramina and relationships of sciuromorphous, myomorphous, and hystricomorphous rodents to these protrogomorphous groups will be the subject of future publications; work on the first of these groups is completed (Wahlert, 1972).

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